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## A Test of the Enemy Release Hypothesis Using a Congeneric Pair of Lespedeza Species

Mary Gail Caflisch

*University of Tennessee - Knoxville*

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To the Graduate Council:

I am submitting herewith a thesis written by Mary Gail Caflisch entitled "A Test of the Enemy Release Hypothesis Using a Congeneric Pair of Lespedeza Species." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology and Evolutionary Biology.

James A. Fordyce, Major Professor

We have read this thesis and recommend its acceptance:

Daniel Simberloff, Nathan Sanders

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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James A. Fordyce  
James Fordyce, Major Professor

Christine R. Boake  
Christine Boake, Department Head

We have read this thesis and  
recommend its acceptance:

Daniel Simberloff

Nathan Sanders

Acceptance for the Council:

Anne Mayhew

Vice Chancellor and Dean  
of Graduate Studies

(Original signatures are on file with official student records)

**A Test of the Enemy Release Hypothesis Using a  
Congeneric Pair of *Lespedeza* Species**

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Mary Gail Caflisch

August, 2006

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## Abstract

The enemy release hypothesis (ERH) postulates that invasive species are released from the effects of the herbivores, predators, pathogens, and other enemies that control population sizes in the native ranges of the invasive species. In a one-year common garden experiment, I compared the native species *Lespedeza capitata* to the invasive species *Lespedeza cuneata*. I examined relative fitness and performance over the first growing season and manipulated arthropod abundance using insecticide applications. While *L. capitata* had higher germination and survivorship than did *L. cuneata*, it also sustained more natural enemy damage. Arthropod reduction increased height and apparent survivorship for *L. capitata*. Consistent with the predictions of the ERH, arthropod reduction did not significantly effect damage, fitness, or performance of *L. cuneata* because natural enemy damage was relatively low for this species as compared to *L. capitata*. I also tested for associational susceptibility, in which one species decreases the fitness of the other by attracting herbivores. Neither species differed in damage when grown together compared to when grown alone, suggesting that associational susceptibility is not a factor for these species. While the predictions of the ERH were supported, ERH may not be the most important factor allowing *L. cuneata* to invade. *L. cuneata* produced an average of 31 seeds per plant, but seed production for *L. capitata* was virtually nonexistent. The comparatively high seed production of *L. cuneata* may contribute more strongly to enhancing population growth than does the increase in survivorship that *L. capitata* experiences when herbivory is reduced.

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# 1. Introduction

Biological invasion is the process by which a species becomes established in an area outside of its historically occurring range (Elton, 1958). Although natural invasions do occur, most current biological invasions are caused by human activity (Williamson, 1996). Invasive species compete with, consume, parasitize, and cause disease in native species. Biological invasions can also alter ecosystem processes such as fire regimes, hydrology, nutrient cycling, and primary productivity. Substantial evidence indicates that invasive species contribute significantly to the extinction of native species (Williamson, 1996; Vitousek, 1997; Loehle, 2003; Sax & Gaines, 2003). One of the most important questions of invasion biology is why some species become invasive when introduced to new ranges, even though they are not problematic in their native ranges, while other introduced species rarely occur outside of cultivation (Elton, 1958). Many hypotheses have been proposed to address this question, several of which implicate arthropod herbivores as significant factors in the success of plant invasions. In this study, I investigate two hypotheses involving interactions between a native and invasive plant species and arthropod herbivores: the enemy release hypothesis and associational susceptibility.

## *The Enemy Release Hypothesis*

The enemy release hypothesis (ERH) posits that some species become invasive because, when they are introduced to a new area, they are not followed by the natural

enemies that control them in their native range (Elton, 1958; Agrawal & Kotanen, 2003; Keane & Crawley, 2002; Wolfe, 2002). The ERH predicts that while native plant populations are substantially regulated by herbivores, invasive species either sustain comparatively less damage by herbivores in their introduced ranges or do not have their fitness substantially regulated by the damage. This hypothesis takes a top-down view of the world in which plant populations are either controlled by higher trophic levels, or the herbivores fail to control the plant populations because the majority of the plant tissue is inedible (Murdoch, 1966).

The ERH is frequently used to explain ability to invade and is often employed as justification for biological control efforts (Williamson, 1996; Devine, 1998; Mack et al., 2000; Wittenberg & Cock, 2001). If a species can become invasive because it has no enemies in its introduced range, then the release of an enemy to control it would be a logical course of action. However, most biological control efforts fail. Only 15% of biological control agents released to combat insect pests and 25% of biological control agents released to combat weeds are considered to have been successful (Baskin, 2002). Some fail to establish in the new habitat, while others establish, but do not affect control of their target species. Regardless of whether a biological control agent successfully controls its intended target, it may have detrimental non-target effects. For example, *Euglandina rosea*, the rosy wolf snail, was introduced to Hawaii as a control agent for the invasive giant African snail, *Achatina fulica*. *E. rosea* has not only failed to control *A. fulica*, it has contributed to the extinctions of at least 15 endemic Hawaiian snail species (Williamson 1996; Devine, 1998). The moth *Cactoblastis cactorum* was introduced from Argentina to Australia in 1925 to control invasive *Opuntia* cactus species. It was so

successful that it was introduced to the Caribbean in 1957. By 1989, the moth had spread to the United States where it attacked native *Opuntia* species, including the endangered species *O. corallicola* (Williamson, 1996; Stiling et al., 2004). Also, cases of successful biological control alone do not validate the predictions of ERH (Keane & Crawley, 2002). Biological control organisms are usually introduced species themselves, and may behave very differently from the way they would in their native ranges. The fact that an enemy can be introduced to control an invasive species is not proof that the lack of such an enemy is the reason the species successfully invaded.

Direct tests of the ERH have taken one of two approaches. The first approach is to compare the abundance and impacts of enemies on populations of an invasive species in its native and introduced ranges. For example, Wolfe (2002) found that *Silene latifolia* was more likely to be damaged by herbivores in its native range than in its introduced range. Fenner and Lee (2001) found a similar result for invasive herbaceous Asteraceae populations in New Zealand as compared to native populations in Britain. Other studies found that diversity and infestation rates by parasites of birds, mammals, amphibians, reptiles, fishes, crustaceans, and mollusks (Torchin et al., 2003) and by fungal and viral pathogens of plants (Mitchell and Power, 2003) are lower in invasive populations than in native populations. The second approach to testing the ERH is to compare the damage sustained by native and invasive species found within the same range, typically as a common garden experiment. This approach tests the prediction of the ERH that invasives species succeed because they sustain little herbivory in their new ranges as compared to species native to that range, which have their population growth regulated by herbivory. Studies of this type are less common and do not show as definitive results as the first

approach. Competition between species has not been tested directly in these studies, only comparative amounts of damage. In the primary example of this approach to testing the ERH, Agrawal & Kotanen (2003) grew congeneric pairs of native and invasive plants in a common garden experiment. Comparing congeneric species decreases differences in herbivory due to phylogenetic differences between the species. The study found that overall, the invasive species experienced amounts of damage equal or greater than that experienced by the native species. Agrawal et al. (2005) then studied the same species for an additional year, to see if this trend remained constant over time. They found that in the second year, invasive species experienced less herbivory than native species, although there was a great deal of variation between congeneric pairs. The authors cited changes in herbivore abundance and plant ontogeny between years as potential factors causing the results to be inconsistent between the two studies (Agrawal et al., 2005). Invasive species also sustained less reduction in growth caused by pathogenic soil microbes (i.e. bacteria and fungi) than did native species, even though the overall biomass of soil microbes was not significantly different. In addition, a species that appeared to escape from one guild of enemies was sometimes more heavily damaged than its congener by a different enemy guild. Agrawal et al. (2005) postulated that fluctuations in abundance of different enemy guilds create windows of opportunity in which the invasive species is not being attacked and can establish.

The predictions of ERH depend heavily on the importance of specialist herbivores in controlling a species in its native range, and evidence of this control is often lacking (Maron & Vilà, 2001). When generalists are more important than specialists in controlling a species, generalist enemies may control the species as it invades a new area.

Because the impact of herbivory may vary from species to species, analyses of the importance of enemy escape for individual problematic species would provide insight in the development of management strategies. For example, such studies might indicate whether biological control is a viable option, or whether treatment with insecticide could provide natives with the benefit they need to exclude invaders.

### *Associational Susceptibility*

Associational susceptibility is the process by which plants experience increased herbivory when growing with neighbors of other species (Brown & Ewel, 1987; White & Whitham, 2000, Stilling et al., 2004). For example, White and Whitham (2000) found that cottonwood trees were more likely to be infested with fall cankerworms when growing in association with box elder, a preferred host of cankerworms. Stilling et al. (2004) demonstrated that the common prickly pear *O. stricta* maintains populations of *C. cactorum*, facilitating damage of *O. corallicola* by *C. cactorum*.

Invasive species have been shown to compete directly with native species for resources (Mack et al., 2000). However, indirect effects such as associational susceptibility may also have important impacts on populations. In some cases, invasive species of plants have been found to attract invasive arthropod herbivores, which may then damage neighboring native plants (Rand & Louda, 2004; Lau & Strauss, 2005). In this way, one invasive species is able to facilitate the invasion of another species, a process which Simberloff and Von Holle (1999) termed “invasional meltdown.” Other interactions which cause invasional meltdown include habitat modification, increased



pollination, and enhanced seed dispersal. The ability of an invasive species to indirectly cause damage to a native species by attracting invasive arthropods may give the invasive species an advantage over the native species, especially if the invasive species is itself experiencing reduced damage because it has escaped its own herbivores. Several examples of associational susceptibility have been examined in previous studies.

Infestation of the native thistle *Cirsium undulatum* by the biological control weevil *Rhinocyllus conicus* has been shown to increase with increasing density of the invasive thistle species *Carduus nutans* (Rand and Louda, 2004). Similarly, Lau and Strauss (2005) demonstrated that the invasive species *Medicago polymorpha* indirectly reduced the fitness of native species *Lotus wrangelianus* by increasing densities of the invasive weevil *Hypera brunneipennis*.

Density may be important for associational susceptibility as well. Root (1973) found that *Phyllotreta cruciferae*, a specialist arthropod herbivore of collards, was more abundant in dense monoculture stands of collard plants as compared to more complex habitats. Root (1973) postulated that when plants grow in dense or nearly pure patches, herbivores are more likely to find and remain on them because the resources the herbivores need are concentrated in one area. Root (1973) termed this process the resource concentration hypothesis.

In this study, I test the prediction of the ERH that the invasive species *Lespedeza cuneata* is less affected by arthropod herbivory in terms of damage, performance, survivorship, and seed production than the native species *Lespedeza capitata*. I examine this in a common garden experiment in which I manipulate arthropod abundance using insecticide. In addition, I test for associational susceptibility between *L. cuneata* and *L.*

*capitata* by investigating whether herbivory on *L. cuneata* increases when it is grown in association with *L. capitata*, and vice-versa.

### *Study Organisms*

In this study, I examined relative levels of herbivory and the impacts of herbivory on performance and fitness of a congeneric pair of *Lespedeza* species. The species used in this study were *Lespedeza cuneata* (Dum.-Cours.) G. Don and *Lespedeza capitata* Michx. (Fabaceae). Both species are perennial forbs, which grow wild in East Tennessee and are found in similar habitats, including roadsides, meadows, and old fields. By using a congeneric pair of species that are similar in form, distribution, and habitat I decrease interspecific differences in chemistry and physiology that affect susceptibility to herbivores (Agrawal & Kotanen, 2003).

*L. capitata*, or round-headed bush clover, is a native North American species found from Florida to Maine, and as far west as Texas and Minnesota. Of the eleven native *Lespedeza* species in the United States, *L. capitata* has the widest distribution (Clewett, 1966). *L. capitata* grows to a height of 0.6-1.5m at maturity (USDA, NRCS, 2006). The seeds and foliage are an important source of food for wildlife, and the plant is considered an excellent forage crop for livestock (Springer et al., 2002). However, Ritchie and Tilman (1995) found that percent cover by *L. capitata* was not affected by exclusion of mammalian herbivores (primarily white-tailed deer, pocket gophers, and small mammals). The effect of arthropod exclusion on this species, to my knowledge, has not been tested.

The invasive species *L. cuneata*, commonly called sericea lespedeza or Chinese lespedeza, is native to Asia. *L. cuneata* grows to a height of 1-1.5m at maturity (USDA, NRCS, 2006) and has a deep taproot that may extend to a depth of over 1m. The species was introduced to North America for erosion control and as a forage crop first in 1896, and then with more success in 1923 (Pieters, 1934; Ohlenbusch & Bidwell, 2001). It is now found throughout most of the eastern United States, from Florida to Michigan and as far west as Texas, where it frequently invades old-field communities and tall-grass prairies (Blair & Fleer, 2002; Brandon et al., 2004). *L. cuneata* is listed as a noxious weed in the states of Colorado and Kansas (USDA, NRCS, 2006) and is considered a “Threat Rank 1” plant in Tennessee by the Tennessee Exotic Pest Plant Council (1996), indicating that the plant is a “severe threat: [an] exotic plant species that possess[es] characteristics of [an] invasive species and spread[s] easily into native plant communities and displace[s] native vegetation.” In states where its use and sale are not restricted by law, this species is often used agriculturally for hay and as a forage crop for livestock. Because it is well adapted to acidic soils and resistant to drought, it can be employed in areas incapable of supporting alfalfa and other forage legumes (Buntin, 1991).

The mechanisms behind the ability of *L. cuneata* to invade natural communities have been explored in several studies but are not yet fully understood. *L. cuneata* is resistant to standard management techniques, such as mowing, grazing, and prescribed burning, and can only be effectively controlled using herbicide (Ohlenbusch & Bidwell, 2001; Blair & Fleer, 2002). *L. cuneata* has a higher ratio of biomass allocation to leaves and a higher specific leaf area than *L. capitata*, which may allow it to invade burned or disturbed areas in which light is not limited (Smith & Knapp, 2001). Brandon et al.

(2004) attributed the plant's success to its ability to shade out neighboring species. Other studies suggest that the tannin-rich residues of *L. cuneata* suppress the growth of several species, including corn, rye, ryegrass, tall fescue, bermudagrass, and bahagrass (Kalburtji & Mosjidis, 1992). *L. capitata* also produces significant tannin concentrations, although the effects of residues produced by this species on competing species have not been studied (Springer et al., 2002). *L. cuneata* also has a more extensive root system than most native prairie species, which gives it an advantage during droughts (Blair & Fleer, 2002).

Herbivory studies suggest that arthropod herbivores do not limit the biomass of *L. cuneata*. Menhinick (1976) described the arthropod fauna of a monoculture stand of *L. cuneata* and characterized the energy flow through the community. The study found that herbivores consumed only 1% of the net primary productivity of the *L. cuneata* plants. The only herbivores that appeared to be food-limited were the nectarivores. Orthopterans and homopterans were the most abundant herbivores in the stand. Buntin (1991) also characterized the arthropod fauna of monoculture *L. cuneata* plots, but in addition, he treated some plots with insecticide, while leaving others untreated. The study found that in untreated plots, although many taxa of arthropod herbivores were present, only the lepidopteran defoliator *Plathypena scabra* (Noctunidae) significantly damaged the *L. cuneata* plants. This species decreased stem height, number of leaves per stem, and dry weight of leaves and stems. Damage by *P. scabra* occurred late in the season, under very high densities of this insect.

## Questions

In this study I address the following questions:

- 1.) Does *L. capitata* sustain more arthropod herbivory than *L. cuneata*?
- 2.) Does *L. capitata* exhibit poorer performance and fitness measures than *L. cuneata* under natural levels of herbivory?
- 3.) Does natural enemy damage determine survivorship or reproductive output for either species?
- 4.) Does reducing herbivory affect performance or fitness measures for either species?
- 5.) Does the magnitude of change in performance and fitness measures caused by reduction of herbivory differ between the two species?
- 6.) Does associational susceptibility increase natural enemy damage for these species?

Two experiments were conducted to address these questions. The first experiment investigated whether a difference exists in the amount of arthropod herbivory experienced by *L. capitata* and *L. cuneata* in the first growing season, and examined differences in survivorship and reproductive output between these species under natural herbivory levels. I also examined whether the amount of herbivory experienced affected survivorship and seed production for the two species. The second experiment involved manipulating the abundance of herbivores to address whether reduction of herbivory improves the performance or fitness for either species. Both species are expected to exhibit increased performance and fitness when herbivory is reduced as compared to natural levels of insect herbivory. However, if the ERH is operating, reducing arthropods

should benefit *L. cuneata* only slightly because it should have “escaped” its enemies, whereas *L. capitata* should benefit greatly from reduced herbivory because its populations are regulated by herbivores. The two species were also grown in mixed-species groups in order to test whether associational susceptibility is a factor for this congeneric pair. If associational susceptibility exists between these two species, either or both species should experience increased damage and exhibit decreased performance and fitness measures when grown in association with each other, as compared to when grown in monoculture.

## 2. Methods

### *Study Site and General Setup*

This study was carried out in an old-field community at the Oak Ridge National Laboratory in Roane County, Tennessee. The site was abandoned from agriculture around 1943. In past years the field has been mowed in spring and fall. *Lespedeza cuneata* occurs naturally in this community, and although *Lespedeza capitata* is not present, the community is consistent with likely habitat for this species. Dominant species include *Lespedeza cuneata*, *Verbesina occidentalis*, *Verbesina virginica*, *Lonicera japonica*, *Solidago altissima*, *Solidago gigantea*, and *Rubus sp.*

A 2-m tall wire mesh fence designed to exclude deer was erected at the field site enclosing a  $36 \times 28$  m experimental area. 160 2-gallon black plastic pots with holes for drainage were buried to the rim of the pot and filled with a 1:1 mixture of Premier Pro-Mix BX potting soil (Premier Horticulture, Quakertown, PA) and Nature's Helper Water Saver Soil Conditioner (Smith Garden Products, Cumming, GA). Pots were arranged in an  $11 \times 13$  grid with two meters between pots in either direction. Potting the plants controlled for differences in soil quality from one side of the field to another, prevented root competition with pre-existing vegetation, and allowed me to be certain of the identity of each individual plant. The latter was especially important to avoid confusion with *L. cuneata* seedlings emerging from the pre-existing seed bank and vegetative shoots of established plants. Potting the plants might also have decreased belowground herbivory, although that effect was not tested.

The field was mowed at the end of April, prior to placement of the pots. The pre-existing vegetation within the field was thereafter allowed to grow in the area surrounding the pots in order to attract a diversity of arthropods similar to what that would be found in a natural old-field plant community. The vegetation was trampled down along each row to one side of the pots to maintain access to the pots. The pots were weeded and kept clear of debris. The pots were watered as needed, which was one to three times a week in May and June, and a single week in September. Otherwise, natural rainfall was sufficient keep the soil moist. Preventing moisture from becoming a limiting resource in this study was important for both species. *L. capitata* is one of the more hydrophilic of the American *Lespedeza* species, particularly in the southeastern extent of its range, although it occurs commonly in dry, open habitats (Clewett, 1966). *L. cuneata* is rather drought-tolerant, due to its deep taproot; however, the plastic pot most likely prevented *L. cuneata* from realizing the full benefit of its root system.

*L. cuneata* and *L. capitata* seeds were purchased from Ernst Conservation Seeds, Meadville, PA. *L. cuneata* seeds were unhulled and unscarified, and were of the common commercial variety. *L. capitata* seeds were of the Rhode Island ecotype.

### *Experiment 1: Comparison of Natural Enemy Damage and Survival between L. capitata and L. cuneata*

In this experiment I examined the underlying predictions of the ERH for this pair of *Lespedeza* species. I addressed whether *L. capitata* sustains more natural enemy damage than *L. cuneata* does and whether *L. cuneata* has higher survivorship and seed



production than does *L. capitata*. I also tested whether higher levels of natural enemy damage decrease survivorship and seed production during the first growing season. The experiment used two species-composition treatments, either ten *L. capitata* or ten *L. cuneata* seeds per 2-gallon pot. There were twenty replicate pots for each treatment, for a total of 40 pots. The first four consecutive rows of pots on the south end of the field were assigned to Experiment 1. Each pot was assigned a to one of the two species-composition treatments using a random number table generated with SAS software (version 9.1. SAS Institute, Cary, North Carolina, USA, 2003). On May 12, 2005, seeds were planted in the pots approximately 0.5 cm below the surface of the soil. The seedlings were exposed to natural levels of arthropod herbivory throughout the growing season.

### **Natural Enemy Damage**

I monitored the plants in this experiment throughout the season, recording germination dates and number of non-cotyledon leaves for each plant weekly until the majority of the seedlings had at least three leaves, at which point the plants were large enough for damage to be quantified. In order to test for differences in herbivory, I visually assessed natural enemy damage from June 3 to September 15, 2005. Seedlings continued to emerge after this date and were scored for damage once they acquired at least one non-cotyledon leaf. I recorded damage weekly in June and July and at two-week intervals in August and September. I recorded the total number of leaves for each plant and counted the number of leaves per plant exhibiting damage. Cotyledons were

not included in the totals. Each leaf was also examined for four natural enemy damage types: chewing damage, small spots of discoloration, large necrotic lesions, and shriveled or misshapen leaves. Chewing damage was most likely inflicted by arthropods; the causes of the other damage types were less certain. The small discolored spots may have been caused by arthropods with piercing or sucking mouthparts. The necrotic lesions may have been caused by a pathogen spread by piercing insects, although the pathogen may have infected the plant through other means. Shriveled leaves may have been caused by a sucking herbivore or a pathogen. Because the observed damage is likely not due exclusively to arthropod herbivores, the term natural enemy damage is used rather than arthropod damage. Damage for each leaf was recorded on a presence-absence basis, and leaves often exhibited multiple damage types. Because plants added new leaves and shed old leaves simultaneously throughout the season, I could not determine which leaves were new since the last sampling date. Thus, repeated measure analysis was not appropriate here because I could not distinguish at each sampling date what damage was new and what had been present on previous sampling dates.

All statistical analyses for this study were performed using JMP software (Version 6. SAS Institute Inc., Cary NC, 1989-2005). There was a significant pot effect ( $P < 0.05$ ) on damage for *L. capitata* on all dates except June 3, June 26, July 10, and Sept. 15 ( $P = 0.1060$ ,  $P = 0.1093$ ,  $P = 0.1243$ , and  $P = 0.4248$ , respectively) and for *L. cuneata* on all dates except June 10, Aug. 1, Aug. 31, and Sept. 15 ( $P = 0.8596$ ,  $P = 0.2289$ ,  $P = 0.3745$ , and  $P = 0.0518$ , respectively). This variation was likely due to differences in moisture and shading among pots. Because the effect was significant for more dates than it was non-significant, pot averages were used for all analyses.

I tested for difference between the two species in damage sustained at each time period by comparing the proportion of leaves that were damaged for *L. capitata* and *L. cuneata* for total damage, small discolored spots, large necrotic lesions, chewing damage, and shriveled or misshapen leaves. I compared each damage type separately to determine whether one damage type was more commonly observed on one species than on the other. Eleven separate Wilcoxon signed-rank tests, one for each sampling date, were conducted for total damage as well as each damage type, employing a sequential Bonferroni correction because damage was not independent among the eleven sampling dates ( $\alpha < 0.05$ ; Holm, 1979). By comparing damage proportions for each date using separate Wilcoxon tests, I was able to examine seasonal damage patterns. Non-parametric analyses were used because the distributions of total damage and the other damage types were non-normal. A finding of higher damage for *L. capitata* is consistent with the predictions of ERH. For dates on which pot effect was not significant, the above Wilcoxon tests were also repeated using individual plant scores, and the results were qualitatively identical to analysis performed on pot means (not shown).

To estimate damage over the entire season, the total damage proportions from each of the eleven time periods were averaged to generate one average damage proportion for each pot. This was done for total damage and for the four recorded damage types. Seasonal means for total damage and for each of the four damage types were compared between *L. capitata* and *L. cuneata* using t-tests. Mean proportion of large necrotic lesions for *L. cuneata* and mean proportion of small discolored spots both had non-normal distributions; the mean proportions for all other damage types had normal distributions. Wilcoxon tests were performed in addition to the t-tests to compare

the means for these two damage types between the two species, and the results were qualitatively identical to the results of the t-tests.

### **Survivorship and Reproductive Output**

Survivorship and reproductive output were used as fitness correlates in this study. To investigate survivorship for each species, I recorded survivorship on the same dates as damage was assessed. To determine whether the survivorship patterns of *L. capitata* and *L. cuneata* differed significantly from each other, I conducted a Kaplan-Meier survivorship analysis. Only plants surviving until the cotyledon stage were included in the analysis. Seeds that did not germinate or that germinated but died before their cotyledons fully developed were excluded.

To investigate reproductive output, I collected seeds in October and November. Seeds were removed from the plants as soon as the seeds reached maturity. A seed was determined to be mature when it hardened and became brown. Because mature seeds generally detached easily from their calyces, any damage to the plant and subsequent plant responses to seed removal were presumed to have minimal effect on further seed production. The seeds were counted and weighed to determine seed set and average mass per seed for each plant.

### **The Relationship Between Damage and Fitness Correlates**

Average total damage was used to as a measure of damage over the course of the season for understanding the relationship between damage, survivorship, and seed

production. I also estimated the maximum damage, or the greatest proportion of leaves damaged at any one time over the course of the season, in order to examine the relationship between damage, survivorship, and seed production. First I determined the highest total damage proportion for each plant out of the total damage proportions for the eleven sampling dates. The highest total damage proportions for each of the plants in a pot were then averaged to create one maximum damage proportion for each pot, representing the average maximum amount of damage sustained by plants in each pot. End-of-season survivorship was calculated by dividing the final number of surviving plants in each pot by the greatest number of plants present in the pot at any one time. This controlled for unequal sample sizes due to varying germination among pots. End-of-season survivorship and maximum damage were rank-transformed because of non-normality (Conover & Iman, 1982). Other transformation methods, including log transformation, were attempted but failed to produce normality, which is why ranked scores were employed.

To investigate the relationship between damage and fitness, two multivariate analyses were conducted. The first was an analysis of covariance (ANCOVA), which investigated the relationship between damage and survivorship for the two species. End-of-season survivorship was used as the response variable and average damage and maximum damage were used as covariates. Interaction terms were initially included but then dropped from the model because of non-significance ( $P > 0.6$  for all). Each species was analyzed separately. A significant species effect suggests that survivorship differed between *L. capitata* and *L. cuneata*. A negative relationship between either of

the damage variables and seeds per plant suggests that increasing damage decreased fitness for these species.

The second multivariate analysis investigated the relationship between damage and seed production for *L. cuneata*. *L. capitata* was excluded from the seed analyses because only one *L. capitata* plant in this experiment produced seeds. The number of seeds produced per surviving plant was averaged for each pot then rank-transformed because of non-normality. Multiple regression was performed with seeds per plant as the response variable and average damage and maximum damage as the predictor variables. A negative relationship between either of the damage variables and seeds per plant suggests that increasing damage decreased reproductive output for this species.

### *Experiment 2: The Effects of Herbivory Reduction and Associational Susceptibility on Performance and Fitness Correlates*

The second experiment involved manipulating arthropod abundance on *L. cuneata* and *L. capitata* grown both alone and in association with each other. In this experiment, I tested whether reducing arthropods affected performance and fitness of the native and invasive lespedeza species and whether this effect was the same for both species. I also investigated the role of associational susceptibility in determining arthropod damage for either species.

*L. cuneata* seeds have a much lower germination rate than *L. capitata* seeds (Koger et al., 2002; M. G. C., personal observation). To ensure that the number of seedlings per pot was constant, rather than planting the seeds directly in the pots in the

field, the seeds in this experiment were germinated in a greenhouse. On May 1, 2005, the seeds were planted in planting trays containing Premier Pro-Mix BX potting soil, at a depth of approximately 0.5 cm, in a greenhouse at the University of Tennessee, Knoxville. The seedlings were transferred to the field on May 26 after four weeks of growth, and transplanted into the remaining nine rows of pots not used in Experiment 1. Only healthy seedlings that were beyond the cotyledon stage of development were used. The seedlings were allowed seven days to recover from the stress of transplanting. Seven *L. cuneata* seedlings died during this period and were replaced with other seedlings from the greenhouse. At the time of transplanting, the *L. cuneata* seedlings were generally smaller and had fewer leaves than the *L. capitata* seedlings because, on average, the *L. capitata* seedlings emerged a full week before the *L. cuneata* seedlings.

To address the question of whether reducing herbivory affected the performance and fitness of either *Lespedeza* species, insecticide was applied to reduce the abundance of arthropods on some of the plants. Sixty pots were randomly assigned to a control group that received no insecticide and were exposed to natural levels of herbivory. The remaining sixty pots were assigned to an arthropod reduction group. Abundance of arthropods was reduced in designated pots by use of permethrin insecticide (Hi-Yield Kill-A-Bug, Voluntary Purchasing Group, Inc., Bonham, TX) applied at a rate of 0.23 L per m<sup>2</sup> every four weeks during June, July, and August. No insecticide was applied once flowering began in September to prevent interference with pollination.

To test for associational susceptibility, four species-composition treatments were used in this experiment. These were monoculture pots consisting of ten *L. cuneata* seedlings, monoculture pots consisting of ten *L. capitata* seedlings, low-density mixed-

species pots consisting of five *L. cuneata* and five *L. capitata* seedlings, and high-density mixed-species pots consisting of ten *L. cuneata* and ten *L. capitata* seedlings. Mixed-species pots allowed for investigation of whether the identities of neighboring plants affected levels of natural enemy damage. Two densities of plants were used to investigate the importance of density for damage, performance, and fitness because plants growing in stands of higher densities have been shown in some cases to attract more herbivores and retain them for longer periods of time (Root, 1973). Therefore, in addition to total number of plants, the number of individuals of each species in a mixed-species pot could affect the amount of herbivory experienced by those plants, especially from specialist herbivores. Seedlings were evenly spaced within the pot, and in the mixed-species treatments, seedlings of the two species were planted in an alternating arrangement.

In summary, there were four species-composition treatments (*L. capitata* monoculture, *L. cuneata* monoculture, low-density mixed-species, and high-density mixed-species pots) crossed with two arthropod treatments (arthropods present and arthropods reduced), for a total of eight treatment combinations (Figure 1). With fifteen replicates for each treatment combination, there were 120 pots total. Each pot was assigned to one of the eight treatment combinations using a random number table generated using SAS software (2003).



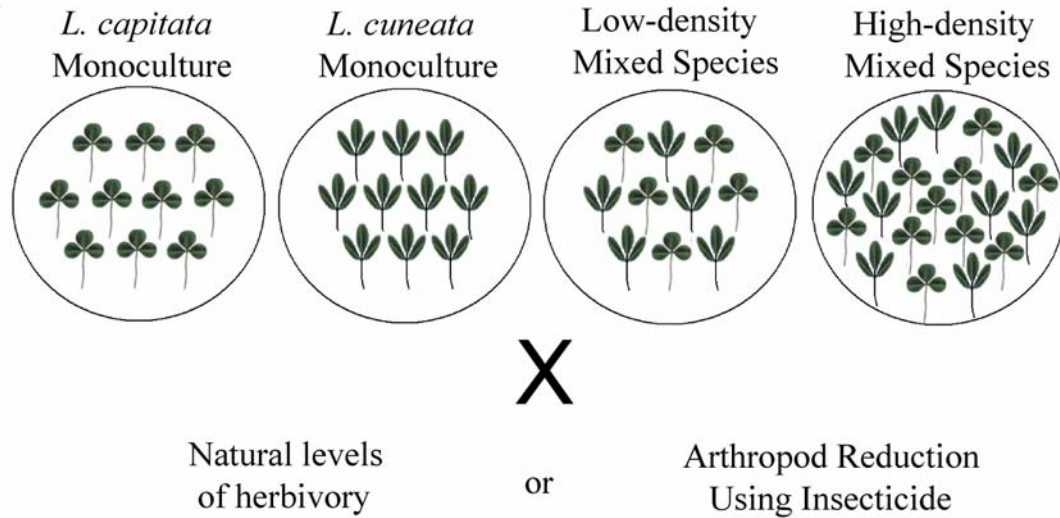


Figure 1. Diagram of the eight treatment combinations used in Experiment 2. Four species-composition treatments – *L. capitata* monoculture, *L. cuneata* monoculture, low-density mixed-species, and high-density mixed-species – were crossed with two arthropod abundance treatments – natural levels of herbivory and arthropod reduction using insecticide – for a factorial design.

### Interspecific Differences and the Effects of Arthropod Reduction

At the end of the growing season in September, measurements were taken for all plants to examine the effect of arthropod reduction on the amount of damage received, performance correlates, and survivorship. Foliar damage was scored on a scale of one to ten, reflecting a combination of the proportion of damaged leaves and the approximate average severity of the damage to the leaves, but was independent of height or total number of leaves. A score of one indicated an apparently undamaged plant, and a score of ten indicated a bare (but living) stem. Dead plants did not receive a damage score, even if aboveground tissue was still present. I measured plant height and counted the

number of primary branches for each plant as performance indicators and proportional survivorship per pot as a measure of fitness.

As in Experiment 1, there was a significant pot effect for damage and height for the majority of the treatment combinations, according to ANOVA ( $P < 0.05$ ). Pot effect was significant about half of the time for number of primary branches. Therefore each pot was considered to be a replicate for each treatment combination. For each of the measured variables, values for each plant within a pot were averaged to produce a single value for each variable for each pot. Survivorship was calculated as the proportion of plants within a pot surviving to the end of the season. Pots containing only one species were given one average score for each of the above variables. Pots containing both *Lespedeza* species were given two average scores for each of the above variables, one for each species.

I first examined the effect of arthropod reduction on damage received, height, and number of primary branches and investigated differences in between the two species regarding these three variables. In this portion of the analysis, I used only the data collected from the monoculture composition treatment pots, eliminating possible interactions between mixed-species and arthropod reduction. A MANOVA was constructed with damage, height, and number of primary branches as the response variables, and species identity, arthropod abundance treatment, and the interaction term as the predictor variables. A significant species identity effect indicates that the species differ from one another with regard to the performance variables. A significant arthropod reduction effect suggests that manipulating the amount of herbivory influenced the performance of these species. A significant interaction between species identity and

arthropod reduction is consistent with predictions of the ERH and can be interpreted as meaning that the species differed from each other in their response to a decrease in herbivory. Subsequently, separate univariate ANOVAs were run for each response variable. The above MANOVA and univariate ANOVAs were repeated using individual plant scores and produced similar results to the analyses using pot means. The MANOVAs and corresponding ANOVAs described above were then produced for each species separately because the species were significantly different from each other in terms of damage received, height, and number of primary branches. This allowed for closer examination of the response of each species to reduction of herbivory, so that differences between the species did not obscure the response.

The ERH predicts that survivorship of *L. cuneata* should not be influenced by the presence of herbivores, but reducing herbivory should increase survivorship of *L. capitata*. Survivorship was rank-transformed because of non-normality, and an ANOVA was constructed with survivorship as the response variable, and species, arthropod reduction, and the interaction term as the predictor variables. As before, separate ANOVAs were produced for each species. In addition, the two arthropod reduction treatments were analyzed with separate ANOVAs to more closely investigate differences between the species at the two levels of arthropod abundance.

### **Associational Susceptibility**

To examine differences between the species-composition treatments (monoculture, low-density mixed, and high density mixed), a MANOVA was constructed

across all treatments. Damage, height, and number of primary branches were the response variables, and species identity, insecticide, species-composition, and all possible interactions were used for the effects. Similarly, an ANOVA was employed using the above predictor variables and with ranked survivorship for the response variable.

Two sets of specific comparisons were then performed to determine whether differences seen here were due to the presence of congeners or density. The first set of comparisons used data from the monoculture and low-density mixed composition treatments, so that total plant density remained constant while presence or absence of congeners varied between treatments. Each species was analyzed separately. A MANOVA was constructed for each species with damage, height, and number of primary branches as the response variables, and an ANOVA was produced for each species with ranked survivorship as the response variable. Species-composition, arthropod reduction, and the interaction term were the predictor variables. Significant species-composition effects here would suggest that the associational susceptibility is operating for this species pair. For the second set of comparisons, the above set of MANOVAs and ANOVAs were produced for each species using data from the low density mixed and the high density mixed composition treatments, so that congeners were present throughout and density varied with composition. A significant effect of species-composition suggests that plant density is important in determining differences between the treatments.

## Reproductive Output

To examine the effects of arthropod reduction and the species-composition treatments on seed production, mature seeds were collected from all of the plants in October and November. The seeds were counted and weighed to determine seed set and average mass per seed for each plant. Only two *L. capitata* plants in this experiment, one in the monoculture natural herbivory treatment, and one in the high-density mixed-species arthropod reduction treatment, set seed, therefore only data from *L. cuneata* were included in the seed analysis.

Average number of seeds per plant was calculated by dividing the total number of seeds produced within a pot by the number of surviving plants in that pot. Number of seeds per plant was rank-transformed due to non-normality. Average seed weight was calculated for each pot by summing the weights of all seeds produced by all plants in a pot and dividing by the total number of seeds for that pot.

The relationship between seeds per plant and seed weight was explored using Pearson's correlation. A MANOVA and corresponding univariate ANOVAs were constructed, with average seed weight and ranked number of seeds per plant as the response variables, arthropod reduction and species-composition, and the interaction term as the predictor variables. A significant species-composition effect suggests that the presence of *L. capitata* influenced seed production in *L. cuneata*. A significant arthropod reduction effect suggests that reducing herbivory affects seed production. The ERH predicts that seed production by *L. cuneata* should not be influenced by herbivory. A significant interaction term suggests that the importance of the presence of *L. capitata* would depend on whether herbivory was reduced, and vice-versa.

In addition, to describe which factors measured in this experiment were the most important in determining seed production, stepwise multiple regression analysis was conducted with seed weight as the response variable and damage, height, number of primary branches, and survivorship as the predictor variables. Then a similar stepwise multiple regression analysis was conducted with the same predictor variables and ranked number of seeds per plant as the response variable.

### 3. Results

#### *Experiment 1:*

Seven *L. cuneata* plants and nine *L. capitata* plants had all leaves and stems removed by herbivores and were excluded from the analyses because standard scoring of damage was ineffective for this type of damage, as the plants had no leaves. Furthermore, it is probable that small mammals, not arthropods, caused this damage. One *L. capitata* pot had its soil upturned by a toad, resulting in the death of all ten plants, and was excluded from the analyses as well.

#### **Natural Enemy Damage**

On each of the eleven sampling dates, *L. capitata* had higher proportions of total damaged leaves and shriveled or misshapen leaves than *L. cuneata* did ( $\alpha = 0.05$ , Figure 2). *L. capitata* had a greater proportion of leaves with small discolored spots on ten sampling dates, a greater proportion of leaves with large necrotic lesions on eight sampling dates, and a greater proportion of leaves with chewing damage than *L. cuneata* on six sampling dates. Proportions of damaged leaves were never significantly higher for *L. cuneata* than *L. capitata* for the four damage types. Most dates on which damage of one of the four types was not different were early in the season.

Seasonal averages for damage showed similar differences between the species. The native species, *L. capitata*, had on average over the course of the season a 57.9% greater proportion of damaged leaves total than did the invasive species, *L. cuneata*. In

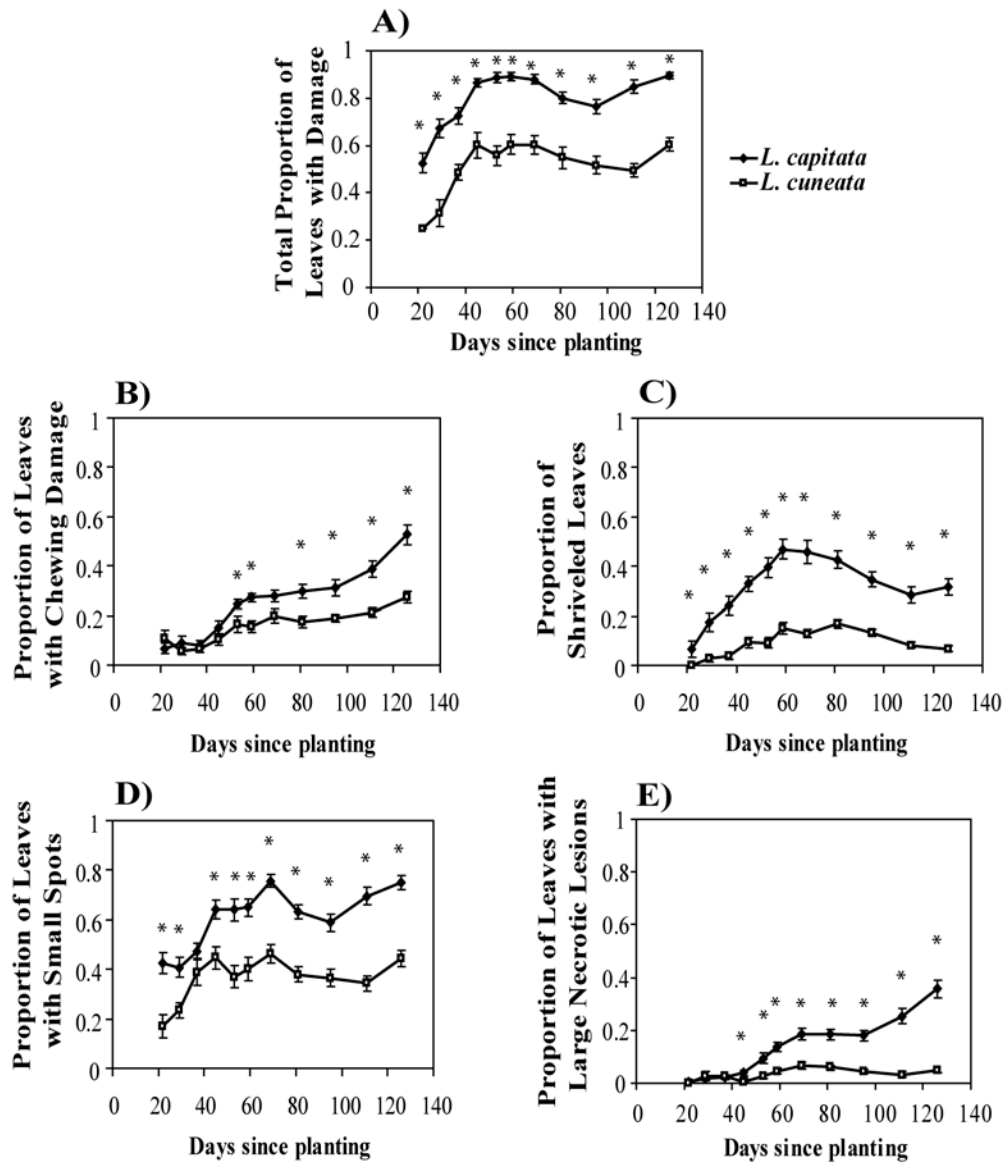


Figure 2. Mean damage scores throughout the season for plants in Experiment 1. Pot averages are shown for *L. capitata* (closed diamonds) and *L. cuneata* (open squares) for each of the eleven sampling dates for (A) total proportion of damaged leaves, (B) proportion of leaves with chewing damage, (C) proportion of leaves that were shriveled or misshapen, (D) proportion of leaves with small spots of discoloration, and (E) proportion of leaves with large necrotic lesions. Error bars are  $\pm 1$  standard error. Asterisks indicate means that are significantly different from each other ( $\alpha = 0.05$ ) according to Wilcoxon tests with a sequential Bonferroni correction.



addition, mean proportions of damaged leaves over the course of the season were higher for *L. capitata* than for *L. cuneata* for all damage types (Table 1).

### Survivorship and Reproductive Output

Germination rate was greater for *L. capitata* (86%) than for *L. cuneata* (54%), (Hypothesis test of difference between proportions:  $z = 7.452$ ,  $P < 0.0001$ ). *L. capitata* had higher post-germination survivorship than *L. cuneata* did, according to Kaplan-Meier survivorship analysis (Fig. 3). 11% more *L. capitata* plants than *L. cuneata* plants survived to the end of the growing season ( $F_{1,35} = 7.8057$ ,  $P = 0.0084$ ), even though *L. capitata* received more damage. Rank-transformed maximum damage sustained did not influence ranked survivorship for *L. capitata* ( $F_{1,16} = 0.0140$ ,  $P = 0.9074$ ) nor for *L. cuneata* ( $F_{1,17} = 1.7115$ ,  $P = 0.2082$ ). Surprisingly, average damage was positively correlated with ranked survivorship for *L. capitata* ( $F_{1,16} = 8.1365$ ,  $P = 0.0115$ ) and *L.*

Table 1. Mean proportions of damaged leaves for *L. capitata* and *L. cuneata* over the course of the season and t-test values comparing mean proportions of damaged leaves for *L. capitata* and *L. cuneata*.

| Damage type                      | <i>L. capitata</i> mean<br>proportion of leaves<br>with damage | <i>L. cuneata</i> mean<br>proportion of leaves<br>with damage | t-Ratio | $P >  t $  |
|----------------------------------|--|---|---------|------------|
| Total damage                     | $0.7669 \pm 0.01889$   | $0.4856 \pm 0.02332$  | 9.372   | $< 0.0001$ |
| Small discolored spots           | $0.5718 \pm 0.02746$   | $0.3577 \pm 0.02284$  | 5.994   | $< 0.0001$ |
| Large spots of necrosis          | $0.1241 \pm 0.1052$  | $0.03328 \pm 0.005079$  | 7.786   | $< 0.0001$ |
| Chewing damage                   | $0.2303 \pm 0.1273$  | $0.1332 \pm 0.00881$  | 6.270   | $< 0.0001$ |
| Shriveled or misshapen<br>leaves | $0.3052 \pm 0.02338$   | $0.07578 \pm 0.008868$  | 9.176   | $< 0.0001$ |

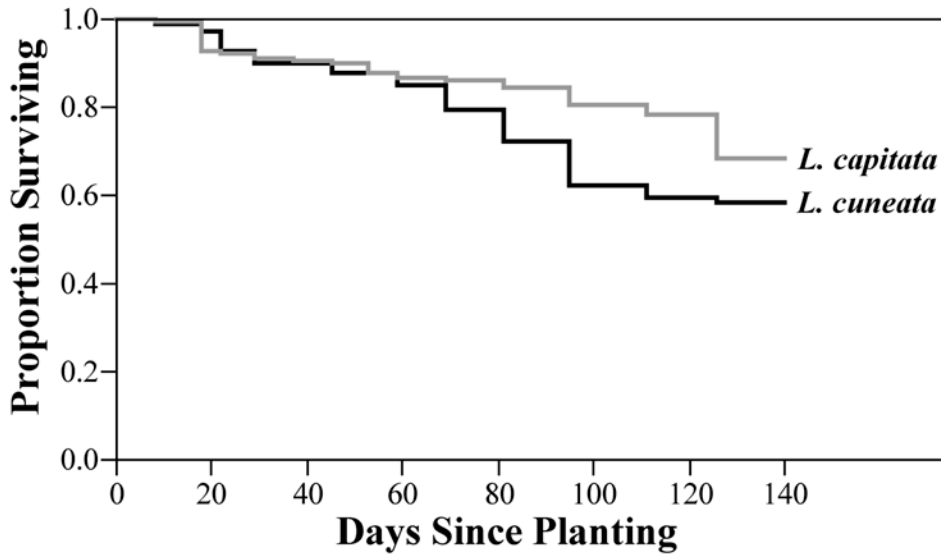


Figure 3. Kaplan-Meier Survivorship Analysis from Experiment 1. Days since planting is shown on the x-axis, and proportion surviving is shown on the y-axis. *L. capitata* is shown in gray, and *L. cuneata* is shown in black. Seeds that failed to germinate were not included in the analysis. Survivorship is significantly different (Kaplan-Meier:  $\chi^2 = 3.9515$ ,  $df = 1$ ,  $P = 0.0468$ ).

*cuneata* ( $F_{1,17} = 15.0516$ ,  $P = 0.0012$ ). The most logical interpretation of this result is that, because damage was cumulative over the course of the season, plants that lived longer tended to accumulate more damage. Damage also did not affect seed production. The ranked number of seeds per plant for *L. cuneata* was not related to average damage ( $F_{1,17} = 2.1616$ ,  $P = 0.1598$ ) or ranked maximum damage ( $F_{1,17} = 1.7780$ ,  $P = 0.2000$ ; additional tables in Appendices).

## *Experiment 2:*

One *L. capitata* monoculture pot in the natural herbivory treatment was excluded from all analyses as none of the plants in this pot survived to the day of data collection. Two mixed-species low-density pots in the natural herbivory level treatment were excluded from the analyses because all of the *L. capitata* plants in these pots failed to survive, although several *L. cuneata* plants in these pots did survive. These pots were included with the mixed-species pots in the seed production analyses, as this did not involve *L. capitata*.

### **Interspecific Differences and Effects of Arthropod Reduction**

The two *Lespedeza* species differed from each other in amount of natural enemy damage sustained, height, and number of primary branches. Reducing arthropods influenced damage and plant height. In the MANOVA of the monoculture composition treatment, species identity and arthropod reduction were both significant factors in the model (Wilks' Lambda = 0.2285092,  $F_{9,129.14} = 11.9681$ ,  $P < 0.0001$ ). Subsequent univariate ANOVAs showed damage, height, and number of primary branches differed between the species (Table 2). *L. capitata* received 60% more damage than *L. cuneata* did. *L. cuneata* plants were 94% taller and had 15 times more primary branches than did *L. capitata* plants (Fig. 4A, B, and C). These results are consistent with previous descriptions of the species (USDA, NRCS, 2006).

Table 2. ANOVAs for the effects of species identity and arthropod reduction on damage, height, number of primary branches, and survivorship in the monoculture composition treatment of Experiment 2.

| Source of Variation                    | DF | Sum of Squares | F Ratio | Prob > F |
|--|----|----------------|---------|----------|
| <b>Damage</b>                          |    |                |         |          |
| Species Identity                       | 1  | 98.136765      | 71.2154 | < 0.0001 |
| Arthropod Reduction                    | 1  | 29.973984      | 21.7514 | < 0.0001 |
| Species Identity X Arthropod Reduction | 1  | 9.060239       | 6.5748  | 0.0131   |
| Error                                  | 55 | 75.79146       |         |          |
| <b>Height</b>                          |    |                |         |          |
| Species Identity                       | 1  | 3652.1658      | 77.3959 | < 0.0001 |
| Arthropod Reduction                    | 1  | 181.3591       | 3.8433  | 0.0550   |
| Species Identity X Arthropod Reduction | 1  | 62.8606        | 1.3321  | 0.2534   |
| Error                                  | 55 | 2595.3446      |         |          |
| <b>Primary Branches</b>                |    |                |         |          |
| Species Identity                       | 1  | 384.23074      | 62.5216 | < 0.0001 |
| Arthropod Reduction                    | 1  | 0.59596        | 0.0970  | 0.7567   |
| Species Identity X Arthropod Reduction | 1  | 0.00034        | 0.0001  | 0.9941   |
| Error                                  | 55 | 338.00599      |         |          |
| <b>Survivorship</b>                    |    |                |         |          |
| Species Identity                       | 1  | 1361.2497      | 5.3342  | 0.0247   |
| Arthropod Reduction                    | 1  | 922.8681       | 3.6164  | 0.0625   |
| Species Identity X Arthropod Reduction | 1  | 301.4450       | 1.1813  | 0.2818   |
| Error                                  | 55 | 14035.499      |         |          |

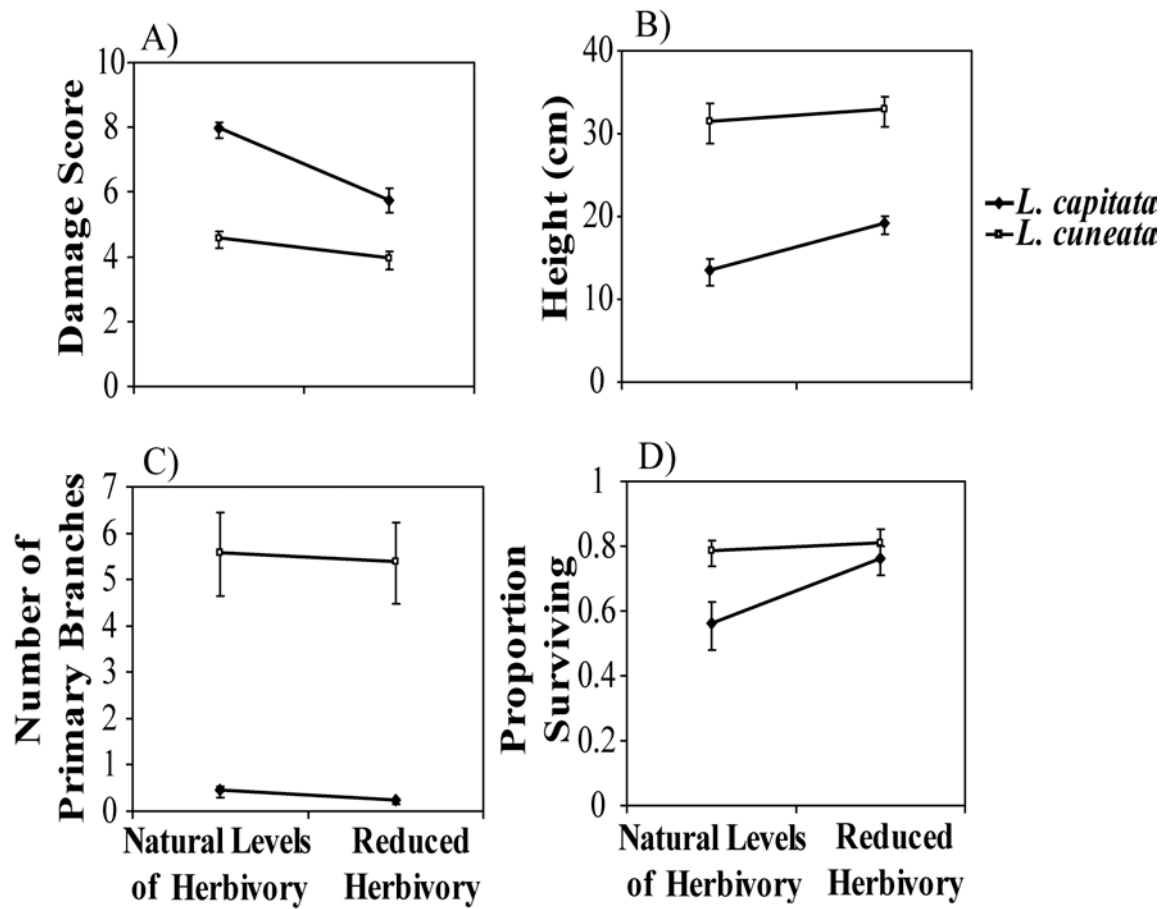


Figure 4. Comparison of means for *L. capitata* and *L. cuneata* between the two arthropod abundance treatments in the monoculture species-composition treatment of Experiment 2. Means are shown for (A) damage score, (B) height in centimeters, (C) number of primary branches, and (D) proportion of plants surviving to the end of the season. Error bars are  $\pm 1$  standard error.

The interaction between species identity and arthropod reduction was significant for the damage response variable. This indicates that reducing arthropods decreased damage experienced by *L. capitata* significantly more than it decreased in damage experienced by *L. cuneata* (Figure 4A). When the two species were analyzed separately (MANOVA:  $F_{3,25} = 7.8008$ ,  $P = 0.0008$ , for *L. capitata* and  $F_{3,26} = 1.4538$ ,  $P = 0.2501$  for *L. cuneata*), *L. capitata* had 28% less damage ( $F_{1,27} = 21.8874$ ,  $P < 0.0001$ ) and 41% greater height ( $F_{1,27} = 8.6299$ ,  $P = 0.0067$ ) with arthropod reduction. In contrast, *L. cuneata* did not differ in damage ( $F_{1,28} = 2.6963$ ,  $P = 0.1118$ ) or height ( $F_{1,28} = 0.2305$ ,  $P = 0.6349$ ) when arthropods were reduced. Arthropod reduction had no effect on number of primary branches ( $F_{1,27} = 2.6397$ ,  $P = 0.1158$  for *L. capitata*, and  $F_{1,28} = 0.0241$ ,  $P = 0.8778$ , for *L. cuneata*).

Differences in survivorship between *L. cuneata* and *L. capitata* depended upon herbivory levels, and the importance of reducing herbivory depended on the species (Fig. 4D). In Experiment 2, *L. cuneata* had 35% higher survivorship than *L. capitata* did. This is in contrast to the findings of Experiment 1, in which *L. capitata* had the higher survivorship of the two species. When *L. capitata* and *L. cuneata* were analyzed separately, arthropod reduction increased survivorship for *L. capitata* by 65% ( $F_{1,27} = 4.4912$ ,  $P = 0.0434$ ), but did not affect survivorship for *L. cuneata* (10% increase;  $F_{1,28} = 0.3305$ ,  $P = 0.5700$ ). When separate ANOVAs were run for arthropod abundance treatments to test the effect of species, *L. capitata* had 42% lower survivorship than *L. cuneata* did under natural levels of herbivory ( $F_{1,24} = 6.3354$ ,  $P = 0.0189$ ). When arthropods were reduced no difference in survivorship was detected between the species

( $F_{1,31} = 0.7411$ ,  $P = 0.3959$ ). These results are consistent with the prediction of the ERH that herbivory should influence survivorship for *L. capitata* but not *L. cuneata*.

### **Associational Susceptibility**

The presence of congeners did not affect damage, height, number of primary branches, or ranked survivorship for either species. The MANOVA using the data from all of the species-composition treatments for *L. capitata* (Wilks' Lambda = 0.5210982,  $F_{15,218.49} = 3.8792$ ,  $P < 0.0001$ ) and *L. cuneata* (Wilks' Lambda = 0.6121409,  $F_{15,221.25} = 2.8699$ ,  $P = 0.0004$ ) was significant. In the univariate ANOVA, damage differed among the composition treatments for both *L. cuneata* ( $F_{2,82} = 3.8184$ ,  $P = 0.0260$ ) and *L. capitata* ( $F_{2,81} = 3.0815$ ,  $P = 0.0513$ ; Fig. 5). Further investigation showed that when only monoculture pots and low-density mixed-species pots were compared and each species was analyzed separately (MANOVA: Wilks' Lambda = 0.498602,  $F_{9,124.27} = 4.5709$ ,  $P < 0.0001$  for *L. capitata*, and Wilks' Lambda = 0.7486018,  $F_{9,126.7} = 1.7786$ ,  $P = 0.0785$ , for *L. cuneata*), species-composition treatment had no effect on damage, height, number of primary branches, or ranked survivorship for either species (ANOVA:  $P > 0.3$  in all cases; Fig. 5A, B, C, and D).

However, density was an important factor in terms of damage for both species, and in terms of height for *L. cuneata*. When low-density and high-density mixed-species pots were compared and each species was analyzed separately (MANOVA: Wilks' Lambda = 0.5757021,  $F_{9,126.7} = 3.5854$ ,  $P = 0.0005$  for *L. capitata* and Wilks' Lambda = 0.6010125,  $F_{9,126.7} = 3.2759$ ,  $P = 0.0013$  for *L. cuneata*), both *L. capitata* and *L. cuneata*

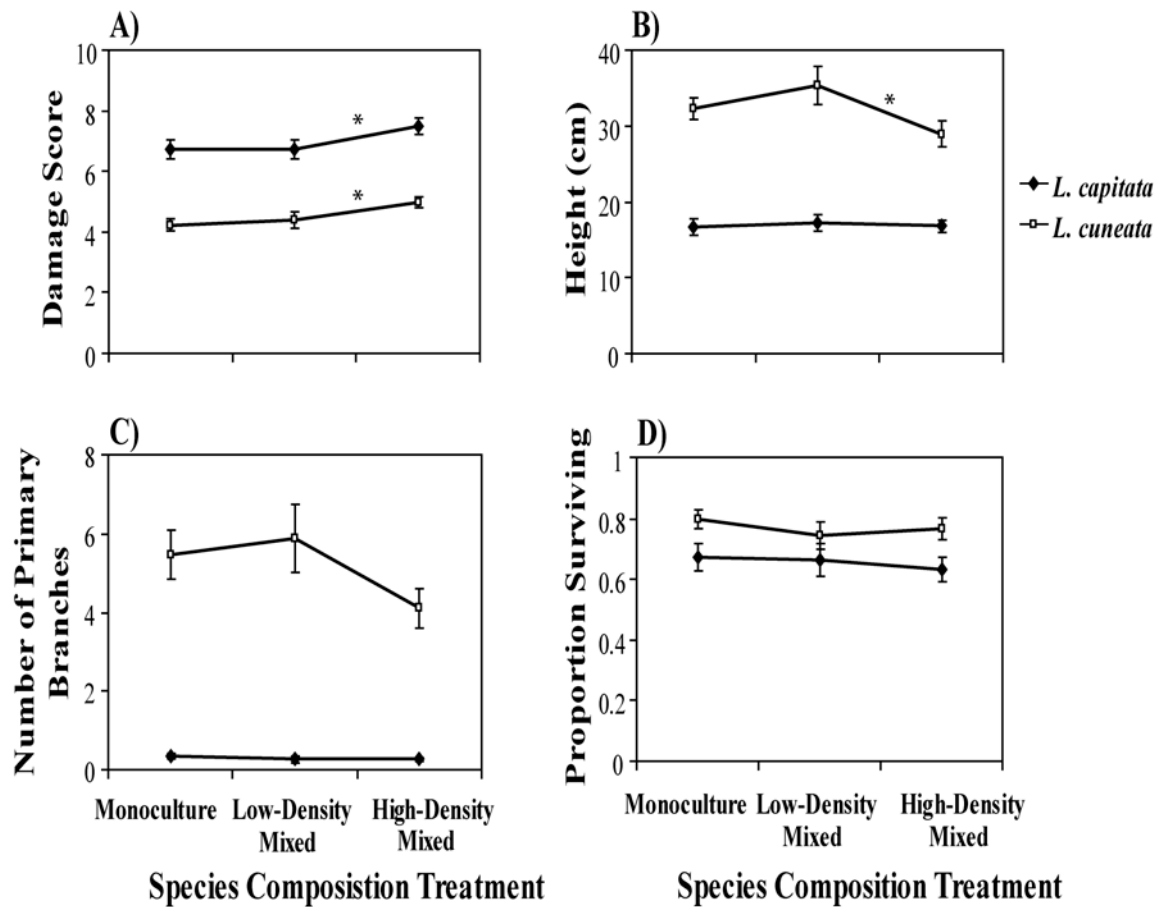


Figure 5. Comparison of means for *L. capitata* and *L. cuneata* among the three species-composition treatments in Experiment 2. Means are shown for (A) damage score, (B) height in centimeters, (C) number of primary branches, and (D) proportion of plants surviving to the end of the season. Asterisks denote statistically different means within each species. Error bars are  $\pm 1$  standard error.



sustained more damage in high-density mixed pots than in low-density mixed pots (12% and 13% more damage, respectively; ANOVA:  $F_{1,54} = 4.8591$ ,  $P = 0.0318$ , and  $F_{1,54} = 3.7446$ ,  $P = 0.0582$ , respectively; Fig. 5A). This is consistent with the predictions of the resource concentration hypothesis (Root, 1973). In addition, *L. cuneata* were 22% taller in low-density mixed pots than in high-density mixed pots ( $F_{1,54} = 4.9684$ ,  $P = 0.0300$ ; Fig. 5B). The interaction between density and arthropod reduction was not significant for *L. cuneata* in terms of damage ( $F_{1,54} = 0.0223$ ,  $P = 0.8818$ ), height ( $F_{1,54} = 0.0182$ ,  $P = 0.8931$ ), or number of primary branches ( $F_{1,54} = 1.0848$ ,  $P = 0.3023$ ), so reducing herbivory had no significant effect on this difference between high and low plant density. There was no difference in height for *L. capitata* ( $F_{1,54} = 0.1153$ ,  $P = 0.7355$ ), nor did the high and low densities differ in number of primary branches ( $F_{1,54} = 0.0132$ ,  $P = 0.9088$  for *L. capitata*, and  $F_{1,54} = 2.9408$ ,  $P = 0.0921$  for *L. cuneata*), or ranked survivorship and ( $F_{1,54} = 0.8962$ ,  $P = 0.3480$  for *L. capitata*, and  $F_{1,54} = 0.0782$ ,  $P = 0.7808$  for *L. cuneata*).

## Reproductive Output

Consistent with predictions of the ERH, seeds per plant and seed weight for *L. cuneata* were not influenced by herbivore reduction or the presence of *L. capitata*. Seed weight was positively correlated with ranked seeds per plant ( $r = 0.3165$ ,  $P = 0.0130$ ). MANOVA (Wilks' Lambda = 0.8900,  $F_{10,108} = 0.6480$ ,  $P = 0.7696$ ) and corresponding univariate ANOVAs found no difference in seed weight or ranked number of seeds per plant among the three composition treatments, nor was there any difference when arthropods were reduced ( $P > 0.1$  in all cases). Stepwise regression was used to

determine which variables (damage, height, number of primary branches, or survivorship) best predicted reproductive output. The stepwise regression included only survivorship in the best model for describing variation of average seed weight ( $F_{1,59} = 2.640$ ,  $P = 0.1095$ ), with seed weight decreasing as survivorship decreased, but not significantly so. The stepwise regression included height ( $F_{1,86} = 4.629$ ,  $P = 0.0342$ ), number of primary branches ( $F_{1,86} = 14.178$ ,  $P = 0.0003$ ), and survivorship ( $F_{1,86} = 12.006$ ,  $P = 0.0008$ ) in the best model for describing variation of ranked number of seeds per plant, with seed number increasing as height, number of primary branches, and survivorship increased.

## 4. Discussion

### *Interspecific Differences*

Although *L. capitata* and *L. cuneata* are closely related and similar in form, habitat, and distribution, they differed in a number of the characteristics measured in this study. *L. capitata* seeds germinated about a week earlier than *L. cuneata* seeds planted at the same time and had a higher germination rate than *L. cuneata* by 32%. *L. cuneata* was significantly taller and had more branches than *L. capitata* did. *L. capitata* always received more damage than *L. cuneata* regardless of time of year or stage of growth. For the most part, *L. capitata* sustained more of each of the different damage types as well. One of the most ecologically important differences between these two species was seed production in the first year. *L. cuneata* plants in these two experiments produced over 10,000 seeds total, an average of about 18 seeds per surviving plant. Several plants produced over 400 seeds each, and one plant produced over 900 seeds. In contrast, *L. capitata* plants across both experiments produced only 35 seeds total (632 surviving *L. capitata* plants, for an average of 0.06 seeds per plant).

Relative survivorship of the two species was not consistent between the two experiments. In Experiment 1, where mortality was closely monitored throughout the season, *L. cuneata* had a higher mortality rate than *L. capitata*, particularly in late July and early August. In addition to herbivory, factors that may be related to this mid-growing season mortality of the invasive species are stress from heat, dehydration, or shading as neighboring vegetation reached its peak height. *L. cuneata* and *L. capitata*

may have responded differently to these stressors. Growing plants in pots may have prevented *L. cuneata* from fully benefiting from its deep taproot, but because the pots were irrigated, lack of water was presumably reduced as a factor. In Experiment 2, in which survivorship was recorded only at the end of the season, *L. capitata* had lower survivorship than *L. cuneata*. The survivorship counts for Experiment 2 were taken approximately two weeks later than were the counts for Experiment 1. During this time, senescence of *L. capitata* species began, and it was difficult to differentiate between death and mere senescence.

### *The Importance of Herbivory*

The ERH predicts that while native species receives more natural enemy damage and suffers greater fitness consequences from that damage, invasive species suffer comparatively lower levels of damage and fitness consequences. In the monoculture treatments of Experiment 2, arthropod reduction decreased damage sustained by the native species *L. capitata* by 28%, but did not significantly reduce damage to the invasive species *L. cuneata*. Interpretations of this result are limited by the fact that not all herbivory was prevented by the insecticide applications. It is probable that a greater effect of reduced herbivory might be seen with increased levels of insecticide. However, it is unlikely that all damage experienced by plants in this experiment was caused by arthropod herbivores. Small vertebrate herbivores, gastropods, fungi, and pathogens were not controlled for and may have accounted for a significant portion of observed damage.

The benefits of reducing herbivory differed greatly between the two species. Since *L. capitata* suffered higher levels of damage, it benefited noticeably when herbivory was reduced. *L. capitata* experienced reduced foliar damage, exhibited increased height, and had increased survivorship when arthropod abundance was reduced using insecticide. Also, reducing herbivory increased apparent survivorship of *L. capitata*, although this might have been due in part to delayed senescence. In fact, under the arthropod reduction treatment of Experiment 2, survivorship of *L. capitata* increased to a level where it was not significantly different from that of *L. cuneata*. These results are inconsistent with those of Experiment 1 in which survivorship was higher for *L. capitata* than for *L. cuneata*. As discussed above, senescence and mortality were indistinguishable in Experiment 2. For this reason, the increase in survivorship in the arthropod reduction treatment as compared to the natural herbivory treatment may be partly due to delayed senescence when arthropods are reduced. It is important to note that *L. capitata* was beginning senescence as *L. cuneata* was beginning the majority of its seed production. It is possible intense levels of herbivory cause premature senescence and reduced seed production for this species. Reducing herbivory might mitigate this effect by allowing *L. capitata* plants additional time to produce seeds. However, in this study seed production of *L. capitata* was too low to draw any conclusions.

Although *L. capitata* benefited from reduced arthropod abundance, *L. cuneata* showed no marked improvements. Because *L. cuneata* received little damage under natural levels of herbivory, reducing herbivory had very little effect on this species. Arthropod reduction did not decrease damage or increase height, number of primary branches, seeds per plant, or seed weight for *L. cuneata*. These results are consistent with

previous experiments in concluding that herbivore damage was not an important factor in the performance and fitness of *L. cuneata*. Menhinick (1967) estimated that herbivorous arthropods consumed between 0.4 and 1.4% of *L. cuneata* primary production. In contrast, the average damage sustained by terrestrial plants has been estimated at around 18% of primary production (Cyr & Pace, 1993). Menhinick (1967) concluded that plant material was not a limiting resource for arthropods feeding in monoculture stands of *L. cuneata*. Buntin (1991) found that, while many species of arthropods were observed feeding on *L. cuneata*, only heavy outbreaks of the lepidopteran defoliator, *Plathypena scabra*, significantly reduced biomass of *L. cuneata*. *P. scabra* occurs in East Tennessee, but was not observed in the high densities described in Buntin's study.

The ERH predicts that invasive species succeed because the invasive populations are freed from the enemies that control their populations in their native ranges. Previous studies have shown that *L. cuneata* is able to outcompete many native species, including *L. capitata* (Blair & Fleer, 2002). The findings of my study indicate that escape from natural enemies may be one reason that this is so. My data support the ERH by demonstrating that, while arthropods present in this field site had an impact on the performance and fitness of the native species *L. capitata*, they had little impact on the performance and fitness of the invasive species *L. cuneata*.

### *Associational Susceptibility*

Associational susceptibility, in which growing the two species together increased the amount of damage sustained by either species, did not appear to be a factor for this

congeneric pair. In comparisons of treatments in which plant density was constant – that is, the treatments with ten of either species were grown alone compared to treatments in which five of each species were grown together, for a constant density of ten plants – there was no difference in damage, height, number of primary branches, survivorship, or seeds per plant for either species. This suggests that neither species increased herbivory on the other species by attracting herbivores.

Although the presence of congeners did not impact damage, performance, or fitness, plant density did have a significant effect, supporting the prediction of the resource concentration hypothesis (Root, 1973) that herbivores are more likely to find and remain in denser patches of plants. In comparisons of treatments with both species grown together at either low (ten individuals) or high density (twenty individuals), both species had less damage in low-density pots. In addition, *L. cuneata* plants in low-density pots were taller, possibly in response to decreased damage, although interspecific competition between the species could be a factor as well. It is possible that a certain threshold number of *L. capitata* plants may be required before foraging arthropods will be attracted to a patch (Root, 1973). If so, the five individuals in the mixed low-density pots may not be enough to increase herbivore visits to the pot. In order to satisfactorily determine whether associational susceptibility plays a role in damage received by *L. capitata* and *L. cuneata*, further testing must be done in which monocultures and mixed stands are grown at higher densities than was done here.

## *Reproductive Output*

While differences in responses to herbivory may be significant for this pair of species, differences in seed production may ultimately be more important for successful invasion by *L. cuneata*. Across all treatments in both experiments, *L. cuneata* produced over 10,000 seeds, while *L. capitata* had virtually no seed production in the first year. Previous studies have found that *Lespedeza* species native to North America sometimes may not flower during the first growing season, and often do not produce as many flowers in the first year as they do during later years (Clewett, 1966). Because seed production for *L. capitata* was so low, I have not attempted to draw any conclusions here about factors influencing reproductive output in this species.

Several factors affected seed production for *L. cuneata*. Although arthropod reduction did not enhance seed production for this species, the taller plants with more branches produced more seeds. Also, plants in pots that had more individuals survive to the end of the season tended to have more seeds per plant, suggesting that conditions favorable for survivorship were also favorable for seed production. Qiu and Mosjidis (1993) showed seed weight of *L. cuneata* was positively correlated with emergence in the field. However, I did not find average seed weight to be related to height, number of primary branches, amount of damage sustained, or survivorship. Only number of seeds per plant was correlated with seed weight.



## Conclusions

My data support the prediction of the enemy release hypothesis for this pair of species in several ways. First, I showed that *L. capitata* received more damage than did *L. cuneata*, both overall, and for the four specific damage types measured. Second, I showed that reducing the abundance of arthropods decreased damage sustained by *L. capitata* but did not significantly reduce the amount of damage sustained by *L. cuneata* because damage to *L. cuneata* was so low overall. Lastly, I showed that *L. capitata* exhibited improved performance and fitness measures when herbivory was reduced, whereas performance and fitness of *L. cuneata* were not affected by herbivory level.

Although herbivores had a substantial impact on *L. capitata*, the native species, while having little or no impact on the invasive species, *L. cuneata*, it is unclear from this study whether degree of herbivory is an important factor in the interactions between these species. While insecticide application decreased damage for the native species, the effect on survivorship was questionable, as mortality might have been confused with senescence in the data. Seed production was the more reliable fitness correlate in this experiment, but because *L. capitata* produced so few seeds, the impact of herbivory on seed production for this species could not be determined.

Damage is not always the most appropriate criterion for predicting fitness, because plants receiving more damage might not necessarily suffer fitness consequences from that damage. Schierenbeck et al. (1994) found that the invasive species *Lonicera japonica* actually produces less biomass when herbivores are excluded. It is likely that seed production by *L. cuneata* is so much higher than that of *L. capitata* that any

difference in fitness caused by herbivory is negligible. Maron & Vilà (2001) suggested that plant populations that have large or long-lasting seed banks might be buffered against years of more intense herbivory. Keane & Crawley (2002) suggested that herbivores may impact individuals but have no effect on populations when recruitment is controlled by other factors, such as seed production, as it appears to be for this pair of species. In conclusion, while the enemy release hypothesis was supported by this experiment, prolific seed production in the first year may be the characteristic that allows *L. cuneata* to invade, not the lack of arthropod herbivores.

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## **Appendices**

## Appendix A: Tables Relating to Experiment 1

Table 3. ANOVA for the effects of average damage, and maximum damage during the first growing season on survivorship in Experiment 1. Each species was analyzed separately. Survivorship and maximum damage values were rank-transformed because of non-normality.

| Source             | DF | Sum of Squares | F Ratio | Prob > F |
|--------------------|----|----------------|---------|----------|
| <i>L. capitata</i> |    |                |         |          |
| Average Damage     | 1  | 7.4378600      | 8.1365  | 0.0115   |
| Maximum Damage     | 1  | 1.27664        | 0.0140  | 0.9074   |
| Error              | 16 | 1462.6219      |         |          |
| <i>L. cuneata</i>  |    |                |         |          |
| Average Damage     | 1  | 1112.2324      | 15.0516 | 0.0012   |
| Maximum Damage     | 1  | 126.4682       | 1.7115  | 0.2082   |
| Error              | 17 | 1256.2122      |         |          |

Table 4. ANOVA for the effects average damage, and maximum damage during the first growing season on seeds produced per plant for *L. cuneata* in Experiment 1. Maximum damage values were rank-transformed because of non-normality.

| Source         | DF | Sum of Squares | F Ratio | Prob > F |
|----------------|----|----------------|---------|----------|
| Average Damage | 1  | 301.13534      | 2.1616  | 0.1598   |
| Maximum Damage | 1  | 247.69678      | 1.7780  | 0.2000   |
| Error          | 17 | 2368.3443      |         |          |



## Appendix B: Tables Relating to Species Identity and Herbivory in

### Experiment 2.

Table 5. MANOVA for the effects of species identity, arthropod reduction, and the interaction term on damage, height, and number of primary branches, in the monoculture species-composition treatment of Experiment 2.

| Source           | DF        | Wilks' Lambda | Sum of Squares | F Ratio | Prob > F |
|------------------|-----------|---------------|----------------|---------|----------|
| a) MANOVA        | 9, 129.14 | 0.2285092     | ...            | 11.9681 | < 0.0001 |
| b) ANOVA         |           |               |                |         |          |
| Damage           | 3, 55     | ...           | 75.79146       | 32.1012 | < 0.0001 |
| Height           | 3, 55     | ...           | 3856.2930      | 27.2406 | < 0.0001 |
| Primary Branches | 3, 55     | ...           | 389.98659      | 21.1527 | < 0.0001 |

Table 6. Canonical coefficients from the MANOVA for the effects of species identity, arthropod reduction, and the interaction term on damage, height, and number of primary branches, in the monoculture species-composition treatment of Experiment 2.

|  | Canonical Coeff. 1 | Canonical Coeff. 2 | Canonical Coeff. 3 | Observed Means $\pm$ Std. Error |
|--|--------------------|--------------------|--------------------|---------------------------------|
| Eigenvalues                            | 2.15229401         | 0.38823194         | 1.72169e-5         |                                 |
| Damage                                 | 0.072409           | 0.08355964         | 0.07211415         |                                 |
| <i>L. capitata</i> , Natural Herbivory |                    |                    |                    | 7.972911 $\pm$ 0.255802         |
| <i>L. capitata</i> , Reduced Herbivory |                    |                    |                    | 5.747272 $\pm$ 0.37423          |
| <i>L. cuneata</i> , Natural Herbivory  |                    |                    |                    | 4.584951 $\pm$ 0.268191         |
| <i>L. cuneata</i> , Reduced Herbivory  |                    |                    |                    | 3.938469 $\pm$ 0.276211         |
| Height                                 | -0.0082031         | -0.0010145         | 0.02680592         |                                 |
| <i>L. capitata</i> , Natural Herbivory |                    |                    |                    | 13.55005 $\pm$ 1.636715         |
| <i>L. capitata</i> , Reduced Herbivory |                    |                    |                    | 19.16171 $\pm$ 1.096885         |
| <i>L. cuneata</i> , Natural Herbivory  |                    |                    |                    | 31.48014 $\pm$ 2.465034         |
| <i>L. cuneata</i> , Reduced Herbivory  |                    |                    |                    | 32.93280 $\pm$ 1.859763         |
| Primary Branches                       | -0.0078732         | 0.0564683          | -0.0462187         |                                 |
| <i>L. capitata</i> , Natural Herbivory |                    |                    |                    | 0.453297 $\pm$ 0.125775         |
| <i>L. capitata</i> , Reduced Herbivory |                    |                    |                    | 0.245982 $\pm$ 0.053435         |
| <i>L. cuneata</i> , Natural Herbivory  |                    |                    |                    | 5.589683 $\pm$ 0.902047         |
| <i>L. cuneata</i> , Reduced Herbivory  |                    |                    |                    | 5.392040 $\pm$ 0.874301         |

Table 7. MANOVAs for the effects of arthropod reduction on damage, height, and number of primary branches, in the monoculture species-composition treatment of Experiment 2, with each species analyzed separately.

| Source             | DF    | F-test Value | Sum of Squares | F Ratio | Prob > F |
|--------------------|-------|--------------|----------------|---------|----------|
| <i>L. capitata</i> |       |              |                |         |          |
| a) MANOVA          | 3, 25 | 0.9360947    | ...            | 7.8008  | 0.0008   |
| b) ANOVA           |       |              |                |         |          |
| Damage             | 1, 27 | ...          | 35.521938      | 21.8874 | <.0001   |
| Height             | 1, 27 | ...          | 225.86458      | 8.6299  | 0.0067   |
| Primary Branches   | 1, 27 | ...          | 0.3082655      | 2.6397  | 0.1158   |
| <i>L. cuneata</i>  |       |              |                |         |          |
| a) MANOVA          | 3, 26 | 0.1677425    | ...            | 1.4538  | 0.2501   |
| b) ANOVA           |       |              |                |         |          |
| Damage             | 1, 28 | ...          | 3.078821       | 2.6963  | 0.1118   |
| Height             | 1, 28 | ...          | 15.5451        | 0.2305  | 0.6349   |
| Primary Branches   | 1, 28 | ...          | 0.28776        | 0.8778  | 0.0241   |

Table 8. Canonical coefficients from the MANOVAs for the arthropod reduction on damage, height, and number of primary branches, in the monoculture species-composition treatment of Experiment 2, with each species analyzed separately.

|                    | Canonical<br>Coeff. 1 | Canonical<br>Coeff. 2 | Canonical<br>Coeff. 3 | Observed Means<br>± Std. Error |
|--------------------|-----------------------|-----------------------|-----------------------|--------------------------------|
| <i>L. capitata</i> |                       |                       |                       |                                |
| Eigenvalue         | 0.93609472            | 0                     | 0                     |                                |
| Damage             | 0.12952996            | 0.09478986            | -0.0036467            |                                |
| Natural Herbivory  |                       |                       |                       | 7.972911 ± 0.255802            |
| Reduced Herbivory  |                       |                       |                       | 5.747272 ± 0.37423             |
| Height             | -0.0084636            | 0.0375912             | 0.02120876            |                                |
| Natural Herbivory  |                       |                       |                       | 13.55005 ± 1.636715            |
| Reduced Herbivory  |                       |                       |                       | 19.16171 ± 1.096885            |
| Primary Branches   | 0.12305072            | 0                     | 0.61323172            |                                |
| Natural Herbivory  |                       |                       |                       | 0.453297 ± 0.125775            |
| Reduced Herbivory  |                       |                       |                       | 0.245982 ± 0.053435            |
| <i>L. cuneata</i>  |                       |                       |                       |                                |
| Eigenvalue         | 0.16774247            | -1.927e-17            | -3.832e-16            |                                |
| Damage             | 0.20662255            | 0.02786321            | 0.11098921            |                                |
| Natural Herbivory  |                       |                       |                       | 4.584951 ± 0.268191            |
| Reduced Herbivory  |                       |                       |                       | 3.938469 ± 0.276211            |
| Height             | -0.0049649            | 0.01583449            | 0.03915097            |                                |
| Natural Herbivory  |                       |                       |                       | 31.48014 ± 2.465034            |
| Reduced Herbivory  |                       |                       |                       | 32.93280 ± 1.859763            |
| Primary Branches   | 0.05114702            | 0.02524225            | -0.0752865            |                                |
| Natural Herbivory  |                       |                       |                       | 5.589683 ± 0.902047            |
| Reduced Herbivory  |                       |                       |                       | 5.392040 ± 0.874301            |

Table 9. ANOVAs for the effects of arthropod reduction on damage, height, number of primary branches, and survivorship in the monoculture species-composition treatment of Experiment 2, with each species analyzed separately. Survivorship was rank-transformed due to non-normality.

| Source              | DF | Sum of Squares | F Ratio | Prob > F |
|---------------------|----|----------------|---------|----------|
| <i>L. capitata</i>  |    |                |         |          |
| Damage              |    |                |         |          |
| Arthropod Reduction | 1  | 35.521938      | 21.8874 | < 0.0001 |
| Error               | 27 | 43.819295      |         |          |
| Height              |    |                |         |          |
| Arthropod Reduction | 1  | 225.86458      | 8.6299  | 0.0067   |
| Error               | 27 | 706.65601      |         |          |
| Primary Branches    |    |                |         |          |
| Arthropod Reduction | 1  | 0.30826552     | 2.6397  | 0.1158   |
| Error               | 27 | 3.1530994      |         |          |
| Survivorship        |    |                |         |          |
| Arthropod Reduction | 1  | 1124.5723      | 4.4912  | 0.0434   |
| Error               | 27 | 6760.6863      |         |          |
| <i>L. cuneata</i>   |    |                |         |          |
| Damage              |    |                |         |          |
| Arthropod Reduction | 1  | 3.0788213      | 2.6963  | 0.1118   |
| Error               | 28 | 31.972169      |         |          |
| Height              |    |                |         |          |
| Arthropod Reduction | 1  | 15.545145      | 0.2305  | 0.6349   |
| Error               | 28 | 1888.6886      |         |          |
| Primary Branches    |    |                |         |          |
| Arthropod Reduction | 1  | 0.28776051     | 0.0241  | 0.8778   |
| Error               | 28 | 334.85290      |         |          |
| Survivorship        |    |                |         |          |
| Arthropod Reduction | 1  | 85.862783      | 0.3305  | 0.5700   |
| Error               | 28 | 7274.8122      |         |          |

Table 10. ANOVA for the effects of species identity on survivorship in the monoculture species-composition treatment of Experiment 2, with each arthropod abundance treatment analyzed separately. Survivorship was rank-transformed because of non-normality.

| Source                             | DF | Sum of Squares | F Ratio | Prob > F |
|------------------------------------|----|----------------|---------|----------|
| <i>Natural Levels of Herbivory</i> |    |                |         |          |
| Species Identity                   | 1  | 1316.3462      | 6.3354  | 0.0189   |
| Error                              | 24 | 4986.6538      |         |          |
| <i>Arthropod Reduction</i>         |    |                |         |          |
| Species Identity                   | 1  | 216.33715      | 0.7411  | 0.3959   |
| Error                              | 31 | 9048.8447      |         |          |

*Appendix C: Tables Relating to Associational Susceptibility in Experiment 2.*

Table 11. MANOVAs for the effects of species-composition treatment, arthropod reduction, and the interaction term on damage, height, and number of primary branches, across all treatments in Experiment 2, with each species analyzed separately.

| Source             | DF         | Wilks' Lambda | Sum of Squares | F Ratio | Prob > F |
|--------------------|------------|---------------|----------------|---------|----------|
| <i>L. capitata</i> |            |               |                |         |          |
| a) MANOVA          | 15, 218.49 | 0.5210982     | ...            | 3.8792  | < 0.0001 |
| b) ANOVA           |            |               |                |         |          |
| Damage             | 5, 81      | ...           | 92.84239       | 10.8808 | < 0.0001 |
| Height             | 5, 81      | ...           | 302.6289       | 2.5150  | 0.0362   |
| Primary Branches   | 5, 81      | ...           | 1.131845       | 1.6918  | 0.1459   |
| <i>L. cuneata</i>  |            |               |                |         |          |
| a) MANOVA          | 15, 221.25 | 0.6121409     | ...            | 2.8699  | 0.0004   |
| b) ANOVA           |            |               |                |         |          |
| Damage             | 5, 82      | ...           | 35.98293       | 6.0417  | < 0.0001 |
| Height             | 5, 82      | ...           | 1451.7319      | 2.8816  | 0.0190   |
| Primary Branches   | 5, 82      | ...           | 67.0669        | 0.9924  | 0.4276   |

Table 12. Canonical coefficients from the MANOVAs for the effects of species-composition treatment, arthropod reduction, and the interaction term on damage, height, and number of primary branches, for *L. capitata*, across all treatments in Experiment 2.

|  | Canonical<br>Coeff. 1 | Canonical<br>Coeff. 2 | Canonical<br>Coeff. 3 | Observed Means<br>± Std. Error |
|--|-----------------------|-----------------------|-----------------------|--------------------------------|
| Eigenvalue                               | 0.77161724            | 0.04669553            | 0.03488037            |                                |
| Damage                                   | 0.07577179            | 0.02881833            | -0.027222             |                                |
| Monoculture, Natural<br>Herbivory        |                       |                       |                       | 7.972711 ± 0.25580             |
| Low-Density Mixed,<br>Natural Herbivory  |                       |                       |                       | 7.847436 ± 0.305533            |
| High-Density Mixed,<br>Natural Herbivory |                       |                       |                       | 8.240646 ± 0.224359            |
| Monoculture, Reduced<br>Herbivory        |                       |                       |                       | 5.747272 ± 0.374230            |
| Low-Density Mixed,<br>Reduced Herbivory  |                       |                       |                       | 5.727778 ± 0.385929            |
| High-Density Mixed,<br>Reduced Herbivory |                       |                       |                       | 6.870015 ± 0.405220            |
| Height                                   | -0.0065328            | 0.02198414            | 7.93123e-5            |                                |
| Monoculture, Natural<br>Herbivory        |                       |                       |                       | 13.55005 ± 1.636715            |
| Low-Density Mixed,<br>Natural Herbivory  |                       |                       |                       | 16.60128 ± 0.952386            |
| High-Density Mixed,<br>Natural Herbivory |                       |                       |                       | 15.25928 ± 1.323571            |
| Monoculture, Reduced<br>Herbivory        |                       |                       |                       | 19.16171 ± 1.096885            |
| Low-Density Mixed,<br>Reduced Herbivory  |                       |                       |                       | 17.70167 ± 1.737163            |
| High-Density Mixed,<br>Reduced Herbivory |                       |                       |                       | 18.18545 ± 0.786997            |
| Primary Branches                         | 0.06003708            | 0.06041184            | 0.29548522            |                                |
| Monoculture, Natural<br>Herbivory        |                       |                       |                       | 0.453297 ± 0.12578             |
| Low-Density Mixed,<br>Natural Herbivory  |                       |                       |                       | 0.432051 ± 0.168890            |
| High-Density Mixed,<br>Natural Herbivory |                       |                       |                       | 0.317177 ± 0.086187            |
| Monoculture, Reduced<br>Herbivory        |                       |                       |                       | 0.245982 ± 0.053435            |
| Low-Density Mixed,<br>Reduced Herbivory  |                       |                       |                       | 0.126667 ± 0.072023            |
| High-Density Mixed,<br>Reduced Herbivory |                       |                       |                       | 0.218676 ± 0.057529            |

Table 13. Canonical coefficients from the MANOVAs for the effects of species-composition treatment, arthropod reduction, and the interaction term on damage, height, and number of primary branches, for *L. cuneata*, across all treatments in Experiment 2

|  | Canonical<br>Coeff. 1 | Canonical<br>Coeff. 2 | Canonical<br>Coeff. 3 | Observed Means<br>± Std. Error |
|--|-----------------------|-----------------------|-----------------------|--------------------------------|
| Eigenvalue                               | 0.45954787            | 0.06133405            | 0.05457669            |                                |
| Damage                                   | 0.09264301            | 0.0657678             | 0.05189579            |                                |
| Monoculture, Natural<br>Herbivory        |                       |                       |                       | 4.585951 ± 0.268191            |
| Low-Density Mixed,<br>Natural Herbivory  |                       |                       |                       | 5.115385 ± 0.378516            |
| High-Density Mixed,<br>Natural Herbivory |                       |                       |                       | 5.634212 ± 0.225145            |
| Monoculture, Reduced<br>Herbivory        |                       |                       |                       | 3.938469 ± 0.276211            |
| Low-Density Mixed,<br>Reduced Herbivory  |                       |                       |                       | 3.791111 ± 0.316766            |
| High-Density Mixed,<br>Reduced Herbivory |                       |                       |                       | 4.396751 ± 0.233230            |
| Height                                   | -0.0052821            | 0.01367252            | 0.00787581            |                                |
| Monoculture, Natural<br>Herbivory        |                       |                       |                       | 21.48014 ± 2.465034            |
| Low-Density Mixed,<br>Natural Herbivory  |                       |                       |                       | 31.1 ± 3.033643                |
| High-Density Mixed,<br>Natural Herbivory |                       |                       |                       | 25.10791 ± 2.371216            |
| Monoculture, Reduced<br>Herbivory        |                       |                       |                       | 32.93280 ± 1.859763            |
| Low-Density Mixed,<br>Reduced Herbivory  |                       |                       |                       | 39.10833 ± 3.694481            |
| High-Density Mixed,<br>Reduced Herbivory |                       |                       |                       | 32.32322 ± 2.089860            |
| Primary Branches                         | 0.02000253            | -0.0324906            | 0.01772105            |                                |
| Monoculture, Natural<br>Herbivory        |                       |                       |                       | 5.589683 ± 0.902047            |
| Low-Density Mixed,<br>Natural Herbivory  |                       |                       |                       | 5.267949 ± 0.792831            |
| High-Density Mixed,<br>Natural Herbivory |                       |                       |                       | 4.596740 ± 0.954885            |
| Monoculture, Reduced<br>Herbivory        |                       |                       |                       | 5.392040 ± 0.874301            |
| Low-Density Mixed,<br>Reduced Herbivory  |                       |                       |                       | 6.423333 ± 1.462491            |
| High-Density Mixed,<br>Reduced Herbivory |                       |                       |                       | 3.675645 ± 0.5010314           |



Table 14. ANOVAs for the effects of species-composition treatment, arthropod reduction, and the interaction term on damage, height, number of primary branches, and survivorship across all treatments in Experiment 2, with each species analyzed separately. Survivorship was rank-transformed because of non-normality.

| Source                            | DF | Sum of Squares | F Ratio | Prob > F |
|-----------------------------------|----|----------------|---------|----------|
| <i>L. capitata</i>                |    |                |         |          |
| Damage                            |    |                |         |          |
| Composition                       | 2  | 10.517565      | 3.0815  | 0.0513   |
| Arthropod Reduction               | 1  | 78.355257      | 45.9147 | < 0.0001 |
| Composition X Arthropod Reduction | 2  | 3.187686       | 0.9340  | 0.3972   |
| Error                             | 81 | 138.22975      |         |          |
| Height                            |    |                |         |          |
| Composition                       | 2  | 8.95892        | 0.1861  | 0.8305   |
| Arthropod Reduction               | 1  | 222.80160      | 9.2579  | 0.0032   |
| Composition X Arthropod Reduction | 2  | 72.95824       | 1.5158  | 0.2258   |
| Error                             | 81 | 1949.3607      |         |          |
| Primary Branches                  |    |                |         |          |
| Composition                       | 2  | 0.11314962     | 0.4228  | 0.6566   |
| Arthropod Reduction               | 1  | 0.89596763     | 6.6960  | 0.0114   |
| Composition X Arthropod Reduction | 2  | 0.15461237     | 0.5777  | 0.5635   |
| Error                             | 81 | 10.838354      |         |          |
| Survivorship                      |    |                |         |          |
| Composition                       | 2  | 1732.4852      | 0.3828  | 0.6831   |
| Arthropod Reduction               | 1  | 6739.7156      | 2.9787  | 0.0881   |
| Composition X Arthropod Reduction | 2  | 6749.1712      | 1.4914  | 0.2311   |
| Error                             | 82 | 185537.28      |         |          |
| <i>L. cuneata</i>                 |    |                |         |          |
| Damage                            |    |                |         |          |
| Composition                       | 2  | 9.096713       | 3.8184  | 0.0260   |
| Arthropod Reduction I             | 1  | 24.905710      | 20.9088 | < 0.0001 |
| Composition X Arthropod Reduction | 2  | 1.980556       | 0.8314  | 0.4391   |
| Error                             | 82 | 97.67522       |         |          |
| Height                            |    |                |         |          |
| Composition                       | 2  | 589.57819      | 2.9257  | 0.0592   |
| Arthropod Reduction               | 1  | 674.56219      | 6.6948  | 0.0114   |
| Composition X Arthropod Reduction | 2  | 186.96326      | 0.9278  | 0.3995   |
| Error                             | 82 | 8262.2120      |         |          |
| Primary Branches                  |    |                |         |          |
| Composition                       | 2  | 47.592867      | 1.7607  | 0.1784   |
| Arthropod Reduction               | 1  | 0.003250       | 0.0002  | 0.9877   |
| Composition X Arthropod Reduction | 2  | 15.915547      | 0.5888  | 0.5573   |
| Error                             | 82 | 1108.2727      |         |          |

Table 13. Continued.

| Source                            | DF | Sum of Squares | F Ratio | Prob > F |
|-----------------------------------|----|----------------|---------|----------|
| Survivorship                      |    |                |         |          |
| Composition                       | 2  | 1732.4852      | 0.3828  | 0.6831   |
| Arthropod Reduction               | 1  | 6739.7156      | 2.9787  | 0.0881   |
| Composition X Arthropod Reduction | 2  | 6749.1712      | 1.4914  | 0.2311   |
| Error                             | 82 | 185537.28      |         |          |

Table 15. MANOVAs for the effects of species-composition treatment, arthropod reduction, and the interaction term on damage, height, and number of primary branches, in the monoculture and low-density mixed-species-composition treatments in Experiment 2, with each species analyzed separately.

| Source             | DF        | Wilks' Lambda | Sum of Squares | F Ratio | Prob > F |
|--------------------|-----------|---------------|----------------|---------|----------|
| <i>L. capitata</i> |           |               |                |         |          |
| a) MANOVA          | 9, 124.27 | 0.498602      | ...            | 4.5709  | < 0.0001 |
| b) ANOVA           |           |               |                |         |          |
| Damage             | 3, 53     | ...           | 66.82762       | 13.1678 | < 0.0001 |
| Height             | 3, 53     | ...           | 238.5230       | 2.8436  | 0.0464   |
| Primary Branches   | 3, 53     | ...           | 1.0284849      | 2.0904  | 0.1125   |
| <i>L. cuneata</i>  |           |               |                |         |          |
| a) MANOVA          | 9, 126.7  | 0.7486018     | ...            | 1.7786  | 0.0785   |
| b) ANOVA           |           |               |                |         |          |
| Damage             | 3, 54     | ...           | 15.800389      | 3.7722  | 0.0157   |
| Height             | 3, 54     | ...           | 600.1909       | 1.7451  | 0.1687   |
| Primary Branches   | 3, 54     | ...           | 12.00977       | 0.2451  | 0.8645   |

Table 16. Canonical coefficients from the MANOVAs for the effects of species-composition treatment, arthropod reduction, and the interaction term on damage, height, and number of primary branches, for *L. capitata*, in the monoculture and low-density mixed species-composition treatments in Experiment 2.

|   | Canonical<br>Coeff. 1 | Canonical<br>Coeff. 2 | Canonical<br>Coeff. 3 | Observed Means<br>± Std. Error |
|---|-----------------------|-----------------------|-----------------------|--------------------------------|
| Eigenvalues                             | 0.88785164            | 0.05467632            | 0.00730011            |                                |
| Damage                                  | 0.09346828            | 0.02066441            | -0.0453847            |                                |
| Monoculture, Natural<br>Herbivory       |                       |                       |                       | 7.972711 ± 0.25580             |
| Low-Density Mixed,<br>Natural Herbivory |                       |                       |                       | 7.847436 ± 0.305533            |
| Monoculture, Reduced<br>Herbivory       |                       |                       |                       | 5.747272 ± 0.374230            |
| Low-Density Mixed,<br>Reduced Herbivory |                       |                       |                       | 5.727778 ± 0.385929            |
| Height                                  | -0.0067982            | 0.02443652            | -0.0070967            |                                |
| Monoculture, Natural<br>Herbivory       |                       |                       |                       | 13.55005 ± 1.636715            |
| Low-Density Mixed,<br>Natural Herbivory |                       |                       |                       | 16.60128 ± 0.952386            |
| Monoculture, Reduced<br>Herbivory       |                       |                       |                       | 19.16171 ± 1.096885            |
| Low-Density Mixed,<br>Reduced Herbivory |                       |                       |                       | 17.70167 ± 1.737163            |
| Primary Branches                        | 0.09224235            | 0.16384164            | 0.28714441            |                                |
| Monoculture, Natural<br>Herbivory       |                       |                       |                       | 0.453297 ± 0.12578             |
| Low-Density Mixed,<br>Natural Herbivory |                       |                       |                       | 0.432051 ± 0.168890            |
| Monoculture, Reduced<br>Herbivory       |                       |                       |                       | 0.245982 ± 0.053435            |
| Low-Density Mixed,<br>Reduced Herbivory |                       |                       |                       | 0.126667 ± 0.072023            |

Table 17. Canonical coefficients from the MANOVAs for the effects of species-composition treatment, arthropod reduction, and the interaction term on damage, height, and number of primary branches, for *L. cuneata*, in the monoculture and low-density mixed species-composition treatments in Experiment 2.

|   | Canonical<br>Coeff. 1 | Canonical<br>Coeff. 2 | Canonical<br>Coeff. 3 | Observed Means<br>± Std. Error |
|---|-----------------------|-----------------------|-----------------------|--------------------------------|
| Eigenvalue                              | 0.24241696            | 0.07326648            | 0.00178428            |                                |
| Damage                                  | 0.12720137            | 0.07451807            | -0.0065498            |                                |
| Monoculture, Natural<br>Herbivory       |                       |                       |                       | 4.585951 ± 0.268191            |
| Low-Density Mixed,<br>Natural Herbivory |                       |                       |                       | 5.115385 ± 0.378516            |
| Monoculture, Reduced<br>Herbivory       |                       |                       |                       | 3.938469 ± 0.276211            |
| Low-Density Mixed,<br>Reduced Herbivory |                       |                       |                       | 3.791111 ± 0.316766            |
| Height                                  | -0.0010925            | 0.01825767            | -0.0063559            |                                |
| Monoculture, Natural<br>Herbivory       |                       |                       |                       | 21.48014 ± 2.465034            |
| Low-Density Mixed,<br>Natural Herbivory |                       |                       |                       | 31.1 ± 3.033643                |
| Monoculture, Reduced<br>Herbivory       |                       |                       |                       | 32.93280 ± 1.859763            |
| Low-Density Mixed,<br>Reduced Herbivory |                       |                       |                       | 39.10833 ± 3.694481            |
| Primary Branches                        | 0.01565201            | -0.0115121            | 0.04211139            |                                |
| Monoculture, Natural<br>Herbivory       |                       |                       |                       | 5.589683 ± 0.902047            |
| Low-Density Mixed,<br>Natural Herbivory |                       |                       |                       | 5.267949 ± 0.792831            |
| Monoculture, Reduced<br>Herbivory       |                       |                       |                       | 5.392040 ± 0.874301            |
| Low-Density Mixed,<br>Reduced Herbivory |                       |                       |                       | 6.423333 ± 1.462491            |

Table 18. ANOVAs for the effects of species-composition treatment, arthropod reduction, and the interaction term on damage, height, number of primary branches, and ranked survivorship in the monoculture and low-density mixed species-composition treatments in Experiment 2, with each species analyzed separately.

| Source                            | DF | Sum of Squares | F Ratio | Prob > F |
|-----------------------------------|----|----------------|---------|----------|
| <i>L. capitata</i>                |    |                |         |          |
| Damage                            |    |                |         |          |
| Composition                       | 1  | 0.074053       | 0.0438  | 0.8351   |
| Arthropod Reduction               | 1  | 66.710290      | 39.4341 | < 0.0001 |
| Composition X Arthropod Reduction | 1  | 0.039537       | 0.0234  | 0.8791   |
| Error                             | 53 | 89.65958       |         |          |
| Height                            |    |                |         |          |
| Composition                       | 1  | 8.94626        | 0.3200  | 0.5740   |
| Arthropod Reduction               | 1  | 159.18555      | 5.6933  | 0.0206   |
| Composition X Arthropod Reduction | 1  | 71.91056       | 2.5719  | 0.1147   |
| Error                             | 53 | 1481.8784      |         |          |
| Primary Branches                  |    |                |         |          |
| Composition                       | 1  | 0.06981085     | 0.4257  | 0.5169   |
| Arthropod Reduction               | 1  | 0.92879342     | 5.6633  | 0.0210   |
| Composition X Arthropod Reduction | 1  | 0.03398339     | 0.2072  | 0.6508   |
| Error                             | 53 | 8.6921336      |         |          |
| Survivorship                      |    |                |         |          |
| Composition                       | 1  | 213.2447       | 0.0748  | 0.7856   |
| Arthropod Reduction               | 1  | 3324.2251      | 1.1656  | 0.2852   |
| Composition X Arthropod Reduction | 1  | 7602.4542      | 2.6658  | 0.1085   |
| Error                             | 53 | 151148.80      |         |          |
| <i>L. cuneata</i>                 |    |                |         |          |
| Damage                            |    |                |         |          |
| Composition                       | 1  | 0.525342       | 0.3763  | 0.5422   |
| Arthropod Reduction I             | 1  | 13.903951      | 9.9585  | 0.0026   |
| Composition X Arthropod Reduction | 1  | 1.644615       | 1.1779  | 0.2826   |
| Error                             | 54 | 75.394573      |         |          |
| Height                            |    |                |         |          |
| Composition                       | 1  | 120.23707      | 1.0488  | 0.3103   |
| Arthropod Reduction               | 1  | 320.43901      | 2.7951  | 0.1003   |
| Composition X Arthropod Reduction | 1  | 153.85375      | 1.3420  | 0.2518   |
| Error                             | 54 | 6190.6839      |         |          |
| Primary Branches                  |    |                |         |          |
| Composition                       | 1  | 1.8023952      | 0.1103  | 0.7410   |
| Arthropod Reduction               | 1  | 3.2837480      | 0.2010  | 0.6557   |
| Composition X Arthropod Reduction | 1  | 6.5536837      | 0.4012  | 0.5291   |
| Error                             | 54 | 882.07637      |         |          |

Table 17. Continued.

| Source                            | DF | Sum of Squares | F Ratio | Prob > F |
|-----------------------------------|----|----------------|---------|----------|
| Survivorship                      |    |                |         |          |
| Composition                       | 1  | 1610.9488      | 0.6052  | 0.4400   |
| Arthropod Reduction               | 1  | 404.4055       | 0.1519  | 0.6982   |
| Composition X Arthropod Reduction | 1  | 118.4261       | 0.0445  | 0.8337   |
| Error                             | 54 | 143749.36      |         |          |

Table 19. MANOVA for the effects of species-composition treatment, arthropod reduction, and the interaction term on damage, height, and number of primary branches, in the low-density and high-density mixed species-composition treatments in Experiment 2, with each species analyzed separately.

| Source             | DF       | Wilks' Lambda | Sum of Squares | F Ratio | Prob > F |
|--------------------|----------|---------------|----------------|---------|----------|
| <i>L. capitata</i> |          |               |                |         |          |
| a) MANOVA          | 9, 126.7 | 0.5757021     | ...            | 3.5854  | 0.0005   |
| b) ANOVA           |          |               |                |         |          |
| Damage             | 3, 54    | ...           | 54.53392       | 10.3973 | < 0.0001 |
| Height             | 3, 54    | ...           | 74.3578        | 1.0770  | 0.3666   |
| Primary Branches   | 3, 54    | ...           | 0.7221432      | 1.6914  | 0.1797   |
| <i>L. cuneata</i>  |          |               |                |         |          |
| a) MANOVA          | 9, 126.7 | 0.6010125     | ...            | 3.2759  | 0.0013   |
| b) ANOVA           |          |               |                |         |          |
| Damage             | 3, 54    | ...           | 28.324150      | 7.7597  | 0.0002   |
| Height             | 3, 54    | ...           | 1435.0897      | 4.0530  | 0.0114   |
| Primary Branches   | 3, 54    | ...           | 61.59174       | 1.4334  | 0.2431   |

Table 20. Canonical coefficients from the MANOVAs for the effects of species-composition treatment, arthropod reduction, and the interaction term on damage, height, and number of primary branches, for *L. capitata*, in the low-density mixed and high-density mixed species-composition treatments in Experiment 2.

|  | Canonical<br>Coeff. 1 | Canonical<br>Coeff. 2 | Canonical<br>Coeff. 3 | Observed Means<br>± Std. Error |
|--|-----------------------|-----------------------|-----------------------|--------------------------------|
| Eigenvalue                               | 0.6646088             | 0.02899704            | 0.01408858            |                                |
| Damage                                   | 0.09441498            | -0.0087268            | 0.04169586            |                                |
| Low-Density Mixed,<br>Natural Herbivory  |                       |                       |                       | 7.847436 ± 0.305533            |
| High-Density Mixed,<br>Natural Herbivory |                       |                       |                       | 8.240646 ± 0.224359            |
| Low-Density Mixed,<br>Reduced Herbivory  |                       |                       |                       | 5.727778 ± 0.385929            |
| High-Density Mixed,<br>Reduced Herbivory |                       |                       |                       | 6.870015 ± 0.405220            |
| Height                                   | -0.0079282            | 0.01944761            | 0.01910681            |                                |
| Low-Density Mixed,<br>Natural Herbivory  |                       |                       |                       | 16.60128 ± 0.952386            |
| High-Density Mixed,<br>Natural Herbivory |                       |                       |                       | 15.25928 ± 1.323571            |
| Low-Density Mixed,<br>Reduced Herbivory  |                       |                       |                       | 17.70167 ± 1.737163            |
| High-Density Mixed,<br>Reduced Herbivory |                       |                       |                       | 18.18545 ± 0.786997            |
| Primary Branches                         | 0.08432231            | 0.26742353            | -0.2301565            |                                |
| Low-Density Mixed,<br>Natural Herbivory  |                       |                       |                       | 0.432051 ± 0.168890            |
| High-Density Mixed,<br>Natural Herbivory |                       |                       |                       | 0.317177 ± 0.086187            |
| Low-Density Mixed,<br>Reduced Herbivory  |                       |                       |                       | 0.126667 ± 0.072023            |
| High-Density Mixed,<br>Reduced Herbivory |                       |                       |                       | 0.218676 ± 0.057529            |

Table 21. Canonical coefficients from the MANOVAs for the effects of species-composition treatment, arthropod reduction, and the interaction term on damage, height, and number of primary branches, for *L. cuneata*, in the low-density mixed and high-density mixed species-composition treatments in Experiment 2.

|  | Canonical<br>Coeff. 1 | Canonical<br>Coeff. 2 | Canonical<br>Coeff. 3 | Observed Means<br>± Std. Error |
|--|-----------------------|-----------------------|-----------------------|--------------------------------|
| Eigenvalue                               | 0.53583214            | 0.0743895             | 0.00834923            |                                |
| Damage                                   | 0.10467218            | 0.01828404            | 0.10403666            |                                |
| Low-Density Mixed,<br>Natural Herbivory  |                       |                       |                       | 5.115385 ± 0.378516            |
| High-Density Mixed,<br>Natural Herbivory |                       |                       |                       | 5.634212 ± 0.225145            |
| Low-Density Mixed,<br>Reduced Herbivory  |                       |                       |                       | 3.791111 ± 0.316766            |
| High-Density Mixed,<br>Reduced Herbivory |                       |                       |                       | 4.396751 ± 0.233230            |
| Height                                   | -0.0064498            | 0.00038916            | 0.01697501            |                                |
| Low-Density Mixed,<br>Natural Herbivory  |                       |                       |                       | 31.1 ± 3.033643                |
| High-Density Mixed,<br>Natural Herbivory |                       |                       |                       | 25.10791 ± 2.371216            |
| Low-Density Mixed,<br>Reduced Herbivory  |                       |                       |                       | 39.10833 ± 3.694481            |
| High-Density Mixed,<br>Reduced Herbivory |                       |                       |                       | 32.32322 ± 2.089860            |
| Primary Branches                         | 0.02099291            | 0.03716694            | -0.0215722            |                                |
| Low-Density Mixed,<br>Natural Herbivory  |                       |                       |                       | 5.267949 ± 0.792831            |
| High-Density Mixed,<br>Natural Herbivory |                       |                       |                       | 4.596740 ± 0.954885            |
| Low-Density Mixed,<br>Reduced Herbivory  |                       |                       |                       | 6.423333 ± 1.462491            |
| High-Density Mixed,<br>Reduced Herbivory |                       |                       |                       | 3.675645 ± 0.5010314           |



Table 22. ANOVAs for the effects of species-composition treatment, arthropod reduction, and the interaction term on damage, height, number of primary branches, and ranked survivorship in the low-density and high-density mixed composition treatments in Experiment 2, with each species analyzed separately.

| Source                            | DF | Sum of Squares | F Ratio | Prob > F |
|-----------------------------------|----|----------------|---------|----------|
| <i>L. capitata</i>                |    |                |         |          |
| Damage                            |    |                |         |          |
| Composition                       | 1  | 8.495291       | 4.8591  | 0.0318   |
| Arthropod Reduction               | 1  | 43.896637      | 25.1076 | < 0.0001 |
| Composition X Arthropod Reduction | 1  | 2.021636       | 1.1563  | 0.2870   |
| Error                             | 54 | 94.41045       |         |          |
| Height                            |    |                |         |          |
| Composition                       | 1  | 2.653979       | 0.1153  | 0.7355   |
| Arthropod Reduction               | 1  | 58.421910      | 2.5386  | 0.1169   |
| Composition X Arthropod Reduction | 1  | 12.011805      | 0.5220  | 0.4731   |
| Error                             | 54 | 1242.7047      |         |          |
| Primary Branches                  |    |                |         |          |
| Composition                       | 1  | 0.00188395     | 0.0132  | 0.9088   |
| Arthropod Reduction               | 1  | 0.58779476     | 4.1301  | 0.0471   |
| Composition X Arthropod Reduction | 1  | 0.15422664     | 1.0837  | 0.3025   |
| Error                             | 54 | 7.6852542      |         |          |
| Survivorship                      |    |                |         |          |
| Composition                       | 1  | 1033.1820      | 0.8962  | 0.3480   |
| Arthropod Reduction               | 1  | 202.7066       | 0.1758  | 0.6766   |
| Composition X Arthropod Reduction | 1  | 1283.7118      | 1.1135  | 0.2960   |
| Error                             | 54 | 62255.738      |         |          |
| <i>L. cuneata</i>                 |    |                |         |          |
| Damage                            |    |                |         |          |
| Composition                       | 1  | 4.556192       | 3.7446  | 0.0582   |
| Arthropod Reduction I             | 1  | 23.647030      | 19.4350 | < 0.0001 |
| Composition X Arthropod Reduction | 1  | 0.027156       | 0.0223  | 0.8818   |
| Error                             | 54 | 65.703056      |         |          |
| Height                            |    |                |         |          |
| Composition                       | 1  | 586.41645      | 4.9684  | 0.0300   |
| Arthropod Reduction               | 1  | 837.33093      | 7.0943  | 0.0102   |
| Composition X Arthropod Reduction | 1  | 2.15215        | 0.0182  | 0.8931   |
| Error                             | 54 | 6373.5234      |         |          |
| Primary Branches                  |    |                |         |          |
| Composition                       | 1  | 42.119222      | 2.9408  | 0.0921   |
| Arthropod Reduction               | 1  | 0.197794       | 0.0138  | 0.9069   |
| Composition X Arthropod Reduction | 1  | 15.536884      | 1.0848  | 0.3023   |
| Error                             | 54 | 773.41982      |         |          |

Table 21. Continued.

| Source                            | DF | Sum of Squares | F Ratio | Prob > F |
|-----------------------------------|----|----------------|---------|----------|
| Survivorship                      |    |                |         |          |
| Composition                       | 1  | 77.7190        | 0.0782  | 0.7808   |
| Arthropod Reduction               | 1  | 3058.6395      | 3.0793  | 0.0850   |
| Composition X Arthropod Reduction | 1  | 2407.3810      | 2.4237  | 0.1254   |
| Error                             | 54 | 53637.097      |         |          |

## Appendix D: Tables Related to Reproductive Output in Experiment 2

Table 23. MANOVA for the effects of species-composition treatment, arthropod reduction, and the interaction term reduction on seed weight and seeds per plant for *L. cuneata* in Experiment 2. Seeds per plant was rank-transformed because of non-normality.

| Source          | DF      | Wilks' Lambda | Sum of Squares | F Ratio | Prob > F |
|-----------------|---------|---------------|----------------|---------|----------|
| a) MANOVA       | 10, 108 | 0.8899981     | ...            | 0.6480  | 0.7696   |
| b) ANOVA        |         |               |                |         |          |
| Seed Weight     | 5, 55   | ...           | 0.1615109      | 0.4053  | 0.8431   |
| Seeds per Plant | 5, 84   | ...           | 3395.879       | 1.0316  | 0.4045   |

Table 24. Canonical Coefficients from the MANOVA for the effects of species-composition treatment, arthropod reduction, and the interaction term reduction on seed weight and seeds per plant for *L. cuneata* in Experiment 2.

|                                       | Canonical Coeff. 1 | Canonical Coeff. 2 | Observed Means $\pm$ Std. Error |
|---------------------------------------|--------------------|--------------------|---------------------------------|
| Eigenvalue                            | 0.08378854         | 0.03673167         |                                 |
| Seed Weight                           | -0.1868547         | 0.46912129         |                                 |
| Monoculture, Natural Herbivory        |                    |                    | 1.7935893 $\pm$ 0.0848603       |
| Low-Density Mixed, Natural Herbivory  |                    |                    | 1.7320383 $\pm$ 0.0807231       |
| High-Density Mixed, Natural Herbivory |                    |                    | 1.7088648 $\pm$ 0.0891634       |
| Monoculture, Reduced Herbivory        |                    |                    | 1.8244136 $\pm$ 0.0874259       |
| Low-Density Mixed, Reduced Herbivory  |                    |                    | 1.7561771 $\pm$ 0.0880264       |
| High-Density Mixed, Reduced Herbivory |                    |                    | 1.6738048 $\pm$ 0.0879188       |
| Ranked Average Seeds per Plant        | 0.00797392         | 0.00038586         |                                 |
| Monoculture, Natural Herbivory        |                    |                    | 55.038462 $\pm$ 7.5668943       |
| Low-Density Mixed, Natural Herbivory  |                    |                    | 44.233333 $\pm$ 6.3137919       |
| High-Density Mixed, Natural Herbivory |                    |                    | 37.178571 $\pm$ 7.6900119       |
| Monoculture, Reduced Herbivory        |                    |                    | 46.529412 $\pm$ 6.0294118       |
| Low-Density Mixed, Reduced Herbivory  |                    |                    | 51.733333 $\pm$ 6.7083577       |
| High-Density Mixed, Reduced Herbivory |                    |                    | 39.28125 $\pm$ 5.7365729        |

Table 25. ANOVA for the effects of species-composition treatment, arthropod reduction, and the interaction term on seed weight and seeds per plant for *L. cuneata* in Experiment 2. Seeds per plant was rank-transformed because of non-normality.

| Source                            | DF | Sum of Squares | F Ratio | Prob > F |
|-----------------------------------|----|----------------|---------|----------|
| <b>Seed Weight</b>                |    |                |         |          |
| Composition                       | 2  | 0.12930460     | 0.8111  | 0.4496   |
| Arthropod Reduction               | 1  | 0.00063187     | 0.0079  | 0.9294   |
| Composition X Arthropod Reduction | 2  | 0.01111051     | 0.0697  | 0.9328   |
| Error                             | 55 | 4.3839264      |         |          |
| <b>Seeds per plant</b>            |    |                |         |          |
| Composition                       | 2  | 2584.3847      | 1.9627  | 0.1469   |
| Arthropod Reduction               | 1  | 2.9677         | 0.0045  | 0.9466   |
| Composition X Arthropod Reduction | 2  | 984.4177       | 0.7476  | 0.4766   |
| Error                             | 84 | 55303.121      |         |          |

Table 26. ANOVA for the effects of damage, height, number of primary branches, and all possible interactions on seed weight for *L. cuneata* in Experiment 2.

| Source                        | DF | Sum of Squares | F Ratio | Prob > F |
|-------------------------------|----|----------------|---------|----------|
| Damage                        | 1  | 0.13710403     | 1.7120  | 0.1964   |
| Height                        | 1  | 0.09672866     | 1.2078  | 0.2767   |
| Damage X Height               | 1  | 0.00147802     | 0.0185  | 0.8925   |
| 1' Branches                   | 1  | 0.12890438     | 1.6096  | 0.2101   |
| Damage X 1' Branches          | 1  | 0.01826889     | 0.2281  | 0.6349   |
| Height X 1' Branches          | 1  | 0.00116676     | 0.0146  | 0.9044   |
| Damage X Height X 1' Branches | 1  | 0.02904076     | 0.3626  | 0.5496   |
| Error                         | 53 | 4.2444257      |         |          |

Table 27. ANOVA for the effects of damage, height, number of primary branches, and all possible interactions on rank-transformed seeds per plant for *L. cuneata* in Experiment 2.

| Source                        | DF | Sum of Squares | F Ratio | Prob > F |
|-------------------------------|----|----------------|---------|----------|
| Damage                        | 1  | 593.5336       | 1.5835  | 0.2118   |
| Height                        | 1  | 8.7925         | 0.0235  | 0.8787   |
| Damage X Height               | 1  | 1004.7527      | 2.6805  | 0.1054   |
| 1' Branches                   | 1  | 8489.5635      | 22.6488 | < 0.0001 |
| Damage X 1' Branches          | 1  | 58.1892        | 0.1552  | 0.6946   |
| Height X 1' Branches          | 1  | 2323.9285      | 6.1999  | 0.0148   |
| Damage X Height X 1' Branches | 1  | 181.6924       | 0.4847  | 0.4883   |
| Error                         | 82 | 30736.411      |         |          |

## Vita

Mary Gail Caflisch was born in Knoxville, TN, on August 2, 1980. She was raised in Blountville, TN, and graduated from Sullivan Central High School in 1998. She received a B. S. in Biology from the University of South Carolina, Columbia, SC, in 2002, where she graduated *magna cum laude* with honors from the South Carolina Honors College. She began her M. S. in Ecology and Evolutionary Biology at the University of Tennessee, Knoxville, TN, in August of 2004. On June 17, 2006, Mary was married to Marcom Allan Nevins whom she met at the University of South Carolina. After Mary completes her M. S., she and her husband will move to Atlanta, GA, where Allan will begin his Ph. D. in Microbiology at Georgia Institute of Technology. Mary intends to pursue a career in environmental education.